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THE STRUCTURE OF THE CENTRAL NERVOUS SYSTEM
OF CORYDALIS LARVA.

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Concerning the insects, many extensive works have been published upon the nervous system from early times down to quite recently. The work of Dujardin, '50, may be said to be a starting point. Numerous papers by Villanes from '87 to '93 give general accounts of the structure, but nothing very definite as to the distribution of individual nerve termination and origin within the ganglia. The extensive work by Saint-Remy, '90, is also a somewhat fragmentary account of numerous forms of tracheate head ganglia. Other earlier papers dealing with cephalic ganglia in particular are those of Newton, '79, and Packard, '80, and in more recent times we have the valuable works of Kenyon, '96, and Haller, '04. In connection with the structure and relationships of abdominal ganglia, the investigations of Binet, '94, and Benedicenti, '95, should be mentioned; and for a summary of the form and structure of the insect nervous system, the general work of Berlese, '97, is invaluable.

Although there are numerous and extensive papers dealing with the structure of insects, very few give a very complete account of the whole nervous system of a single species and practically no single work treats of the larval centers in much detail, although numerous papers take up the development and some as Bauer, '04, consider the transformations of larval into the adult conditions.

The external anatomy and general distribution of ganglia and nerves of *Corydalid* have been studied by Krauss, '84, and by Hammar, '08. The relations of the trachea to the nervous system and their distribution within it by Hilton, '09. The

present paper is a continuation of the study of the nervous system in the larval form and, although not as complete as might be wished, it is at least a start in the direction of a clearer comprehension of the insect central nervous system, undertaken for the purpose of preparing for a study of the finer structure of the nerve cells, and for experiments upon their metabolism and function.

The methods employed were various. For obtaining the best idea of the general distribution of nerve cells and fibers, and the tracts of which they are parts, *intra vitam* methylene blue injections were used. Beautiful results were obtained at times, but it was only after hundreds of specimens were gone over that much was learned as to the organization of the ganglia. Sectioning methods with the usual fixers and stains gave fair results and the methods of Golgi and Cajal were tried, also those of Villanes and Kenyon. All of these gave good preparations except the Golgi method which I hope to try again at another time. There were difficulties in the way of fixing and staining because the ganglia are inclosed in chitin and because of the numerous tracheal vessels, and in the larger ones it was not possible to get perfect whole mounts. Sketches were made from the methylene blue preparations both before and after fixation and in the first stages of the work peripheral nerves were traced by means of gross dissections.

ABDOMINAL GANGLIA.

The abdominal ganglia, eight in number are quite uniform in appearance and general structure with the exception of the eighth or most caudal. The first abdominal is separated by only short connectives from the third thoracic, and the seventh is even closer to the eighth. The seven first abdominal ganglia have quite uniformly on each side, two large nerve trunks connected with them, a cephalic lateral and a ventral more caudal branch. The eighth ganglion has four pairs of branches leading into it from the caudal end of the animal.

Specimens were injected with methylene blue and nerves traced to the periphery and from here followed into the ganglia as nerve tracts as far as possible. In an earlier study on the nervous system of larval insects I found that in some cases some of the more cephalic branches connected with the ganglia were in large part if not totally sensory, that is arising from

bipolar nerve cells and nerve plexuses, from tactile hairs and from the surface of the hypodermis. In *Corydalis* at various times during several years I have tried to determine the motor and sensory parts of each peripheral trunk for the purpose of following them into the central nervous system. To some degree methylene blue stain is of a differential value in determining the nature of nerve trunks, for very often the first neurons to take the stain are sensory, while motor fibers and cells are often slower to turn blue. But this method is not absolutely sure, for there is great variability in the staining reactions of different individuals. The only sure way of telling whether a given branch is motor or sensory is by tracing the nerves to their endings in muscle fibers or from their origin in bipolar sense cells at the periphery. The tracing of a motor or a sensory nerve or tract is not possible in a large number of cases because the stain is incomplete or too dense, but occasional selectively stained preparations enable one to make positive if not complete statements in regard to nerve trunks; that is to say, one can determine surely from a specimen that a large number of branches of a certain nerve are all motor or all sensory, but it would be impossible to say with *perfect* assurance that the nerve was pure motor or pure sensory because some fine terminations might remain uncolored, especially in the case of a stain which was good for sensory terminations, for there would be a strong probability that some at least of the fine motor ends would not show.

The work of Hammar, '08, on the nervous system of *Corydalis* has been very helpful, and the general description of the nervous system given by him is so complete that I shall not need to spend time on the gross anatomy of the various ganglia, and in speaking of the several branches of the ganglia I shall follow his terminology.

There are three chief branches breaking from the *Lateral* trunk of each of the first seven abdominal ganglia, their method of branching from this trunk and from each other is somewhat variable, but these three main parts are easily recognized. Branch 2 is large and comes off quite near the base of the lateral trunk, runs caudally a short distance and then disappears between muscle fibers in a ventral direction. I could not determine it to be anything but a motor branch although some of the fibers from it are among the first to stain and some of them pass not into the ganglion connected with the nerve

trunk, but run directly up to the next ganglion by the way of the connectives, in a tract which from its other connections in other species and in this form, and from its staining reactions, I took to be sensory. Branch 3 is long, it runs up to the dorsal side of the animal and is without doubt mixed motor and sensory, containing fibers which supply dorsal muscles and fibers which come from the hypodermis. Branch 4 runs into the lateral appendage and seems to be sensory, for the most part at least. Besides these, there are two minute branches, 1 and 5, running out to the trachea, according to Hammar, '08.

The ventral trunk runs caudally and ventrally, branches 1, 2 and 3 run to more and more caudal portions of the ventral side of the animal and seem to be entirely sensory, branch 3 runs to some extent also into the lateral appendage, while branch 4 runs into the tracheal gill and was the only one traced into it. So this whole ventral trunk seems to be for the most part sensory.

The eighth abdominal ganglion seems to be made up of at least two centers fused, there are four main trunks entering it on each side below and all of these so far as could be determined are both motor and sensory. Trunk (a) is most lateral, (b) a ventral trunk corresponding to the ventral one of other abdominal ganglia, (d) a more median one supplying lower dorsal and ventral portions of the body and (c) median, with a large branch which runs back up the intestine.

NERVE CELLS.

(Fig. 5.)

The nerve cells of the periphery have already been figured in an earlier article, Hilton '02. The functional cells of the ganglia both thoracic and abdominal appear to be much of the same type in methylene blue preparations, uni- or bipolar nerve cells, one of the processes or branches of which may run out quite a long distance before they break up into a number of terminations, the other portion usually breaks up into branches near the cell body. Indications of multipolar cells were seen in some specimens but with these usually all of the processes but one were very small and hard to trace very far. In addition to the functional neurones of both large and small size, there were in all of the ganglia, numerous neuroblasts, or smaller cells with slight protoplasm about the nucleus, and neuroglia networks.

NERVE TRACTS IN ABDOMINAL GANGLIA.

(Figs. 1 and 2.)

By means of methylene blue preparations it was possible in some more deeply stained specimens to trace the main tracts of fibers within the ganglia and within the connectives and in lighter stained specimens the distribution of special tracts and even individual fibers. At times the cells stained as well as the fibers at other times only fibers were colored.

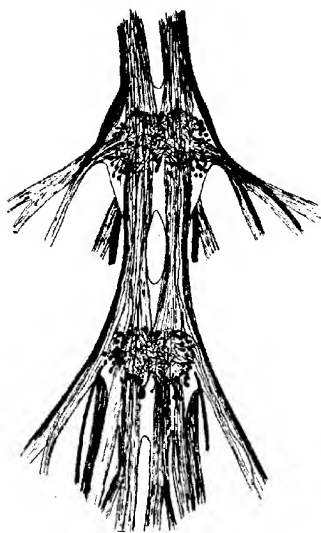


Fig. 1.

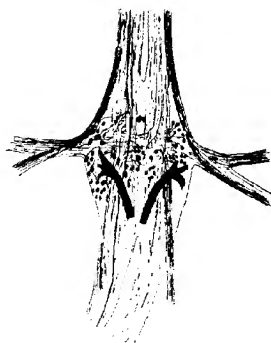


Fig. 2.

FIG. 1. Figure of the 7th and 8th abdominal ganglia from methylene blue preparation. Dorsal side. A few nerve cells are shown in black. The chief nerve trunks show with their fibers. The central "Punktsubstanz" of the ganglia dotted. Some of the larger tracheal tubes shown as thick solid black lines.

The caudal end is down in this and the following figures. x30.

FIG. 2. Sixth abdominal ganglion from ventral side. Methylene blue. x30.

Stained or unstained, the central region of each ganglion is more opaque or darker, due to the nerve fibers crossing and terminating in this region. This forms on each side a central body made up of two oval masses more or less fused into one at the middle line, the "Punktsubstanz" of some authors. The

nerve fibers of the connectives when stained in a mass form deep lines apparently running straight through the center of the ganglia, these longitudinal bundles of nerve fibers seem to be a little broader before entering and after leaving the central mass. The nerve trunks in deeply stained specimens send masses of fibers into the ganglia and in the case of most of the fibers, the region where they seem to terminate is in the central part of each ganglion. This is true of all the ventral fibers and of most of those from the lateral trunk, but a few of the latter, and some fibers from the second branch of the lateral, run up into the edge of the ganglion only, and then straight up the connective to the next ganglion above. In the case of the eighth abdominal the four nerve trunks enter the fibrous central mass from below, those most medially placed seem to be continued up through to the connectives and to be largely continuous with them in deeply stained specimens, while the more lateral trunks are lost sight of as they enter the central portion of the ganglion, although *some* of the fibers from the more laterally placed nerve trunks pass through the edge of the ganglion without communication with its cells and pass up the outer side of the connectives on either side to the next ganglion above. There are then two masses of fibers entering each center but the last, those of the connectives and those of the nerve trunks. I will first take up those of the connectives.

Beginning with the seventh abdominal ganglion great masses of fibers enter, and it is possible to distinguish; (a) Fibers which run straight through without terminating. There seem to be great numbers of these, but this is due *in part* to the fact that when fibers *do* terminate in a ganglion they end at various levels. These fibers can however individually in a number of cases be traced through a ganglion without endings of any sort within it, just how far some of these may run without termination is a question, but there was no difficulty in tracing them through three ganglia and there is no reason to doubt that they may be longer than this. Those most easily followed were usually of larger size than the rest. (b) Fibers from below, terminating within the ganglion. Of these there are several sorts: (1) Those ending in the lower part of the "punksubstanz" on the same side. (2) Those ending on the same side above. (3) Those crossing over towards the opposite side from below. (4) Those crossing over to the opposite side above.

In those entering from below some run straight in and end in the caudal region of the central fibrous mass, while in many specimens fibers from the outer side of the connectives sweep sharply in towards the center of the lower part of the ganglion to end near the middle line, either on the same side or just over it. (c) Fibers from above. In general there are similar bundles of fibers to those traced from below: (1) Those ending in the lower part of the ganglion on the same side. (2) Those ending on the same side but in the cephalic portion of the ganglion. (3) Those crossing to end in the lower part. (4) Those crossing to end in the upper part.

In the case of fibers ending in the ganglion from the cephalic direction, none were seen forming such a dense sweep into each center from the sides of the connectives, although there were a few fine ones of this sort. Most of the fibers leave the "punksubstanz" to run in the connectives without great deviation from a straight course. (d) Fibers passing into the connectives from cells within the ganglion. There may be distinguished in many of the preparations cells with their fibers well stained, the more central of these may be more clearly seen in some cases. Some of the larger more central cells seem to be merely for association within the ganglion, with all of their processes ending within it. Others send one main process up one connective and another down into one of the other great masses of fibers. Other cells of medium or small size, located chiefly at the sides of the ganglion send one long process into one of the nerve trunks while the other shorter process may run for a short distance in the connective trunk or be lost in the central mass of the ganglion.

THE FIBERS OF NERVE TRUNKS.

These have already been spoken of to some degree. Most fibers of both cephalic and ventral nerves seem to enter the central part of the ganglion and are lost track of in the "Punktsubstanz," but both the lateral and ventral trunk-fibers are continued into the connectives in the cephalic direction at least, and possibly to some extent in the caudal, although this was not determined. In the case of the lateral trunks of all the abdominal ganglia, there is a possible sensory tract entering the cephalic edge of the nerve center without coming to the central "punksubstanz" or having any communication with

nerve fibers, running along the outer side of the connective and for the most part ending in the basal portion of the ganglion next above, near or across the middle line. A similar tract to this has been described coming from the two most lateral trunks in the last ganglion.

These fibers which enter from cephalic lateral trunks seem to stain among the first and in the case of some other insects were found to come from bipolar sensory cells at the periphery, and I still think that they are to some extent sensory, but these tracts which have no communication with the cells of the ganglia with which they are connected are not *all* of the sensory fibers of each nerve center, for the ventral branches have many sensory fibers and these do not follow exactly the same path, and in the case of the first seven abdominal ganglia many of the fibers could be traced from the branch 2, which so far as could be determined was a decidedly motor trunk.

Fibers other than those coming from cells on the opposite side to run into the branches as motor axones, are directly supplied by cells on the same side, long branches from certain cells run into the various motor trunks while the other terminations are in the "punksubstanz."

Fibers from the periphery or from sensory cells enter the ganglion from both main trunks and are of the following groups: (a) Those ending within the ganglion to which the trunks are connected, the exact termination of these I could not make out, but some at least ended near the central part of the ganglion, although very often arborizations of the terminations could be traced both on the same side and on the opposite side. Fibers entering straight from below in the last abdominal broke up into branches near the middle line with arborizations in the central margin of the ganglion.

(b) Those passing from one ganglion to the next without sending branches to the center to which the nerve trunks are connected, some of these fibers may run past one or more ganglia, but the most of them form a definite tract from the periphery by way of lateral trunks, running on the outside of the connectives, and turning sharply in towards the middle line in the caudal portion of the central mass of fibers, to end here or a little higher up, or to cross over and end in the "punksubstanz" of the opposite side not far from the middle line.

(c) Those passing from the periphery into the nerve trunks and having extensive arborizations in the ganglia to which they are connected and then passing on to another ganglion with arborizations in it. Only a few of such fibers were distinguished and one in connection with the 8th ganglion was the clearest case. A nerve fiber from the periphery was easily traced into the 1st. lateral trunk, a branch from this fiber was given off in the cephalic and lateral region of the ganglion, this fiber could be traced into the "punktsubstanz" of the nerve center, some of its arborizations ending on the same side and one branch was traced to the cephalic region of the other side, while the main fibers passed up the connective and ended by arborizations in the "punktsubstanz" of the ganglion next above chiefly on the same side in the caudal region.

ABDOMINAL GANGLIA STUDIED IN SECTION.

Individual cells and fibers were not so easily traced by this method, but general masses of fibers and the location of cell groups were determined.

All of the ganglia, connectives and nerve trunks are inclosed in a chitinous envelope which in many cases is very close to the nervous tissue but usually separated by neuroglia cells. This envelope is especially thick about the connectives just before and just after they enter a ganglion, it appears as a uniform mass in section with large and smaller openings where trachea penetrate it.

In places under the chitin of the ganglia, especially on the dorsal side, there are large spaces with little or nothing in them but delicate neuroglia networks. The trachea radiating in the chitin covering the connectives and ganglia have already been referred to; as stated in a previous paper large branches and fine tracheoles run to the nervous system and are distributed to all centers and their branches. These are superficial or run in the chitinous sheath, and the deep, supplied in part by the superficial twigs but chiefly by larger special branches and enter the ganglion and connectives. In these connectives it is easy to see numerous openings, large and minute between the masses of nerve fibers, and in cross section the air tubes are shown to be fully as numerous as one would expect from a study of surface views where all the trachea were made to show. Tracheal tubes within the ganglia are particularly noticeable

in the centers of bundles of fibers and most easily seen in these traced from the connectives. The exact place and method of termination was not determined. Injections of fluids into the ganglia by way of trachea failed to penetrate any of the finer branches.

All of the abdominal ganglia seem to be of practically the same type, but individual variations occur.

In all of the nerve centers the cells are grouped for the most part on ventral and lateral portions of the ganglion and towards the caudal end, a few cells occur on the dorsal side especially near the middle line and these are often quite large.

Description of 4th abdominal ganglion traced by sections beginning at the caudal end:

The connectives entering from the ventral side are easily followed as distinct longitudinal masses of fibers well up into the ganglion, these connectives as well as others in other parts of the nervous system are composed of numerous closely packed longitudinal fibers, scattered between these are the openings of trachea, when the ganglion is reached the chitin for each of the connectives becomes fused into one mass and farther in the central portion of chitin between them disappears and the two bundles of fibers are more or less crowded against each other. Farther up into the ganglion the fiber bundles do not occupy all of the area under the chitin because large spaces on all sides occur and then soon cells in a single layer are found close to the wall of the ventral side, and then on the dorsal side a very large cell is found wedged in between the two bundles of fibers. Some of the cells of the ventral side may be seen at this level sending fibers into the two longitudinal bundles. The single layer of cells on the ventral side becomes a double row of medium and small, and the large cell of the dorsal side gives way to a group of small ones and there comes to be on the ventral side two groups of fibers running more transversely, probably made up in part from fibers connected with the cells appearing on the ventral side.

Farther up these ventral nerve cells extend out laterally so that numbers of them might be seen from the dorsal side. No cells are left for a distance on the mid-ventral line, and they disappear from the mid-dorsal line also to some extent, but before they are gone fibers can be traced about the connective bundles and to the cell region of the ventral side. At this

level there are nerve fibers seen between the cells on the ventro-lateral margins of the ganglion and fibers connected with these regions of the nerve center join the bundle from the cells on the dorsal side, on the ventral median side of the ganglion, while a third runs in from these cells into the central part of the longitudinal fibers. We have then at this level three transverse bundles of fibers crossing from the lateral cell groups, a dorsal, a ventral and median and a little farther along we have also a bundle of fibers running across the section but from the dorsal to the ventral side and uniting to some degree with the three right and left commissures. Other little branches from these main ones and other tracts from the lateral cell groups also invade the longitudinal bands from the connectives.

A little above this level again on the ventral side a single layer of cells appears in the middle line and no cells are seen on the dorsal side except laterally.

A little above this, the large ventral trachea enter passing through the cell layer and breaking up into numerous branches. The central fibrous mass of the ganglion is largely made up of longitudinal strands in all levels so far and besides the commissures mentioned there are usually a number of fibers crossing irregularly both dorso-ventrally, laterally and obliquely especially at about this last level. None of them are large and the great mass of fibers remains longitudinal. It is at about this level that the ventral nerve trunks come off from the lateral and ventral sides of the ganglion from the central part of the latero-ventral cell mass, just before the tracheal trunks are reached. Fibers from this trunk may mingle with the cells of this region and are also continued into the central mass of fibers of the ganglion.

Beyond this point the cells become thin again especially ventrally and also laterally, the central thickest part of the ganglion is now reached and the fibers form a rather large dense mass. Longitudinal ones may still be seen mixed in with numerous lateral and transverse strands all bound up together into a dense fibrous mass with no very marked special tracts or strands except for quite a well marked short broad median commissure of fibers connecting more intimately the two already well fused masses of each lateral half of "punksubstanz."

Slightly beyond this, the cells have about disappeared, only a few remaining at the dorso-lateral edges of the ganglion.

Beyond this something of the central commissure remains, many of the other crossed fibers in the central part of the ganglion have disappeared. A bundle of fibers partly transverse and partly fused with the central longitudinal bands begins to be seen on either side of the ganglion ventrally, these are partly mixed with the main longitudinal tracts. They are endings of the bundles of the lateral nerves to be followed later and might be called lateral nerve tracts. At this level a few scattering cells on the ventral side and two small dorso-lateral groups, one on each side of the ganglion indicate about all of the cell masses seen lower down, while in the mid-dorsal line a new group of dorsal cells makes its appearance and sends fibers *through* the central part of the ganglion as a central tract which breaks up laterally and can be traced to various parts of the central fiber mass of the ganglion. For several sections these fibers become quite prominent and the central commissure seems to be lacking, then as this central tract disappears higher up, another and a better marked commissure comes to view running transversely through the center of the ganglion from side to side. At this level cells again come into view laterally. The ventral tracts of the lateral nerves become more prominent and there is a dorsal band of fibers close to the edge of the "punksubstanz" on the dorsal side. This last is parallel with the median.

Slightly beyond this a few cells are seen on the ventral side laterally, two of the same commissures, a dorsal and a median may be seen, but the lateral cells have disappeared to give place to the entrance of the fibers of the large lateral nerves. These fibers for the most part run directly into the lateral nerve tract noted above when it was seen more caudally. Beyond this and beyond the entrance of the lateral nerve, a few cells are seen laterally, one or so in the mid-dorsal line, and the dorsal and median connectives disappear and only a few tangled fibers replace them, although for a few sections the great sweep of transverse fibers is continued from side to side, from the lateral nerve tract.

Above this no commissure or cross fiber of any sort connects the lateral halves of the ganglion and a small group of nerve cells comes to lie on the middle line and dorsal and ventral to it. At the line of separation of the lateral halves, the tracts of the lateral nerves can be distinguished as a dense mass on either

le of the longitudinal fibers which are continued out into the connectives.

Above this as the cells disappear and we come clearly into the region where there are only longitudinal tracts, these may be followed and they are indistinguishable from other fibers of the connectives. The reason why the lateral tracts could be told from the longitudinal for such a distance was because they seemed denser and stained more deeply. The fibers in the cephalic connectives have about the same arrangement as the caudal ones.

In other abdominal ganglia, ventral and lateral groups of nerve cells were more clearly seen contributing to the commissures and the central tracts. Some of the fibers of the lateral trunks end in the central portion of the ganglion, probably in cells.

The tract of the lateral trunk needs a word of additional comment. In preparations made by a method that removes the cells and all but the denser fibers so that little more than a skeleton of the fibrous framework is left, it is found that a transverse portion connecting the two sides of the ganglion is *much* denser than other parts of the fibrous mass and under the highest powers of the microscope, this seems to be very finely granular as well as fibrous and is continuous from side to side between the nerve trunks. This same fine granular substance with fibrils in it was traced up into the connectives a short distance, and as many fibers are seen to end in this region it may be due to a dense grouping of their endings that there is a deeper color at such a place. Similar substances to this only in more isolated portions is found in other parts of the ganglion and in other nerve centers. In specimens stained with ordinary hematoxylin there is no differentiation between this substance and the general fibrillar mass.

The eighth abdominal ganglion is similar to the others except that the connective fibers begin *within* the ganglion and there are more commissures developed. The first lateral branch can be easily traced out into the connective on the outside, fibers also deeper in go on up the connective, while still others enter the ganglion and are distributed to all parts of one side and probably also across to some extent, as there are numerous cross connections, by means of at least three or four well marked commissures, besides irregular fibers. Other

branches also send fibers to the central mass, some of these run straight through, while others seem to cross in commissures or end.

In general then, there are in each abdominal ganglion, cells on the ventral caudal region, on the lateral sides, and a few on the median dorsal side. These cells surround a central fibrous mass made up of strands running longitudinally through the ganglion from the connectives and best marked in the cephalic and caudal parts; fibers running across from side to side, these run in about three commissures, a dorsal, a ventral and a median and at various cephalic and caudal levels these commissures are interrupted. The lateral nerve trunks may be seen to contribute largely to the formation of the large ventral commissure. The other cross connections seem to be more exclusively from cells on the sides of the ganglia and from these cells also other cross or diagonal fibers may be followed.

The dorsal group of cells which seems to be to a large degree for association, sends fibers through the ganglion to the cells of the lateral and ventral groups, so that these fiber tracts may be found above or below the commissures penetrating to the opposite side, or part way through when the median commissure is present.

THORACIC GANGLIA.

Methylene blue method. (Fig. 3).

The three thoracic ganglia are quite a little larger than the abdominal and the branches come off differently.

There are on each side three main trunks the most cephalic of these has its most cephalic branches pure sensory, but No. 2 was not determined, also No. 1 of trunk B or the middle trunk seems sensory while other branches of the middle trunk are more or less mixed and the last which goes into the leg is also mixed. So then the more cephalic nerves are sensory while the rest seem to be mixed. The exact nature of the two parts of the last or leg branch was not determined, but there was no reason from the staining reactions to indicate that they were of greatly different composition.

In the thoracic region as in the abdominal, the main trunks easily took up the stain, but here greater difficulty was encountered in surface studies because of the larger opaque mass of the ganglion. Cells and fibers were however made out and found

be in a general way similar to the conditions found more caudally. The main tracts of the connectives and of the nerve trunks enter the central portion of each center as in the abdominal region, but their distribution within was harder to make out. There were tracts entering the last thoracic ganglion from below, leaving it again as in the abdominal centers.

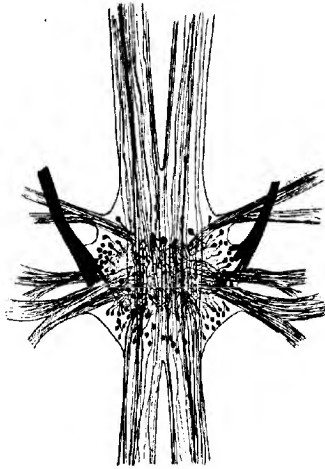


Fig. 3.

Fig. 3. Third thoracic ganglion from below. Methylene blue. x30.



Fig. 4.

Fig. 4. Connective branch leading off between the 2d and 3d thoracic ganglia, nerve fibers from above and below enter the nerve trunk from the connective. Also large and small nerve fibers shown. Methylene blue. x45.

Tracts from the first abdominal pass up the outside of the connective and cross over into the middle line, but from the third thoracic to the second, and from the connectives of the second to the first no such tract was clearly recognized. Fibers entering laterally both from motor and sensory nerves all pass in towards the central part of the ganglion. In other words there was no indication of a tract passing from cephalic branches into the edge of the ganglion to run without termination up the outside of the connective to the next center. But there was an indication of fibers passing through or into one ganglion from the one below it.

In the cephalic part of the thoracic ganglia fibers coming from above may some of them be traced as a fine tract ending

in the cephalic portion of the ganglion. Other than the differences, there were no essential ones between these nerve centers and those of the abdominal region.

In regard to the arrangement of cells as shown by methylene blue, it was found that the lower ventral and lateral regions had the greatest number, great masses of them, with many more cells than in the smaller ganglia. For the most part similar arrangements of individual fibers were seen. Nerve cells sending fibers directly into motor trunks, cells of medium or rather small size, were observed, but these were few in number. Most of the cells seen had their processes running into the "punksubstanz" of the ganglion. Large and smaller association cells were found as in the lower regions and of various sorts such as already described for them, some at the surface of the ganglion other at the edges of the "punksubstanz."

Between the third and second and the second and first thoracic ganglion, there are branches off from the connectives, a pair between each of these, and between the subesophageal and the first thoracic there are two pairs. The upper of these last were not so well stained in any of the preparations but all of the others were quite well colored and found to be motor. These branches when studied as to their composition did not differ much from each other and in each one, fibers could be seen descending to run out the nerve trunk from the ganglion next above and also from the ganglion below. These two tracts of fibers entering the lateral trunks were clear and distinct from each other for quite a distance into the nerve trunk. (Fig. 4).

THORACIC GANGLION IN SECTION.

(Plate XV, Figs. 1-4.)

The internal structure of the thoracic ganglia is much more complicated than the abdominal, due to the fact that the larger branches from the more numerous nerve cells are more intimately woven together, and it was practically impossible to follow commissures or tracts very far except in a very general way. However, a general description as detailed as seems necessary will be given of one of the thoracic ganglia, the first.

From above the connectives which enter as in the abdominal ganglia are in every way similar. Not many cells are seen scattered in the upper part of the ganglion, then two large

groups appear one on each side laterally and a small ventral group. (Fig. 1-3, Plate I). These masses at the sides of both large and small cells are at least three deep. The three groups a little farther along become united by a single row of cells which farther up becomes double layered and all the cell groups are not distinguishable in the single mass. There are also at about this level as a part of this mass a few cells in the mid-ventral line between the bundles of fibres of the connectives.

Farther up, the connective tracts are less clearly *all* longitudinal fibers and the lateral part of the nerve cell mass gives way for the entrance of the first or most cephalic of the three nerve trunks, the fibers of which pass into and mingle as transverse and dorso-ventral fibers in the connective tracts. The fibers of this nerve are very extensive and may be followed into the center of the ganglion, both dorsally and ventrally. Fibers from the ventral cells on either side of the ganglion enter the center of each lateral half from below and are there lost and partly pass into the nerve trunk. Fibers from the cells in the mid-ventral line, which cells form a wedge shaped mass at higher levels between the connective masses, run to the dorsal side of each of these masses of longitudinal fibers, and from here circle about to become associated with the fibers of the nerve trunks and with other more median strands on each side of the ganglion and with the strands described above which come from the ventral mass. Slightly beyond this part and nearer the center of the ganglion the two central masses of fibers or connective masses become fused together, the cells disappear and commissures, a dorsal, a ventral and a median, connect to some degree the sweeps of fibers already described. (Fig. 4, Plate XV, just above this level.)

Farther down, two commissures, a median and a dorsal are seen but numerous fibers cross the middle line at many levels and angles. Farther on but one commissure can be noted, a ventral, but many other fibers cross at different angles and the whole lateral portion of the ganglion is a dense system of complicated interlacing fibers having a dense meshwork. On the lateral part of each ventral half the fibers stain darker, probably due to more numerous fine branches in this region and on the dorsal median line a little wedge shaped group of cells makes its appearance, the only cells of this region. These send their fibers through the center of the ganglion to the ven-

tral side, while a central commissure crosses these to end in the tangled mass of fibers on either side of the ganglion. Farther along, these dorso-ventral bands a little one side of the middle line do not cross the now larger central commissure, but run in to it as do the other fibers from the ventral side, running from the more deeply stained ventral mass already spoken of.

Farther along and at the level of the next nerve, three commissures, a ventral, a dorsal and a median may be again recognized while the fibers of the middle nerve both end in the lateral portions of the fibrous mass and contribute to the three commissures. In this level only a few scattering nerve cells were seen. Beyond this a ventral, almost a lateral group appears again on each side and fibers from these form a little arch about the now smaller mass of darker staining fibers. On the mid-dorsal line fibers from this arch and others from these cells also ramify into all parts of the ventral portion of the ganglion. Along from this the dorsal part comes to be separated into two separate masses of longitudinal fibers of the connectives again. Farther along the arch becomes in its dorsal portion fused into a median commissure which soon disappears as the cleft between the connectives becomes deeper and reaches way down to the now small area of deeply staining substance which now forms a ventral commissure. The ventral cell group has become more lateral at this level and another large group has come in just dorsal to it, but still only on the side. In the mid-ventral line also, there has come in a small new group of cells.

The last nerve trunk comes to be associated with this commissure of deeply staining fibers on the ventral side and farther along fibers also pass freely into it from the lateral group of cells which has been spoken of as coming in more dorsally, this for a time remains distinct from the other more ventral groups.

Along farther these cell groups unite to form a large thick single lateral mass and from them more fibers run into the commissure of deeply staining fibers and "Punksubstanz."

Soon after this the commissure breaks through as the two connective bundles separate, each with a little of the darkened mass which soon disappears as do the cells of the ganglion.

Although the above description is only a very general one, it will be seen that the ganglion is more complicated than the abdominal, but the general plan of arrangement and structure is as in the abdominal region. The nerve cells as in the abdomi-

ganglia are chiefly grouped in the caudal, cephalic and ventral regions and may be seen to take direct part in the formation of commissures as well as diagonal strands. While dorsal cells on the median line and ventral median cells, send fibers through the ganglion dorso-ventrally, as well as association fibers to different tracts and lateral groups. In both thoracic and abdominal ganglia dark staining masses made up of very minute fibers fused together are chiefly found on the ventral side and associated with a ventral commissure.

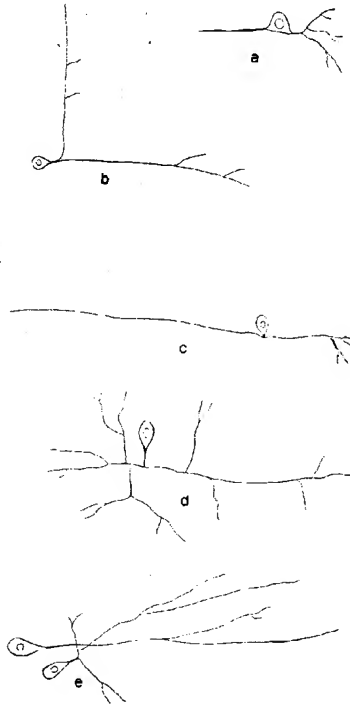


Fig. 5.

FIG. 5. Nerve cells from the central nervous system. (a) Motor nerve cell from the 3d thoracic ganglion. (b, c and d) Association cells from the same. (e) Cells from the brain. x100.

THE SUBESOPHAGEAL GANGLION.

(Figs. 6 and 7, Plate XVI, Fig. 5.)

This ganglion is larger than the others described, and is less flattened and less easy to study from the surface. The branches have already been traced quite well to the periphery and I will only mention them briefly.

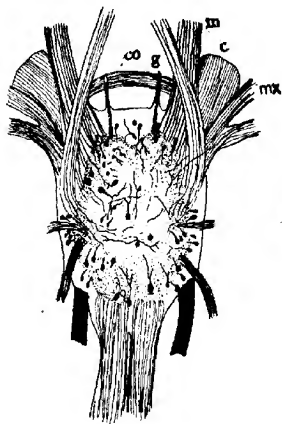


Fig. 6.

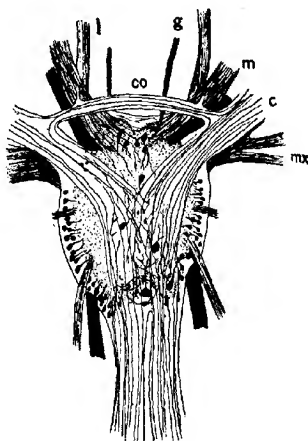


Fig. 7.

FIG. 6. Subesophageal ganglion from the ventral side. Methylene blue, x30.

c.....connective with brain.
co.....commissure
mx.....maxillary
m.....mandibular
l.....labial
g.....gustatory

FIG. 7. Subesophageal from the dorsal side. x30.

The caudal portion of the ganglion becomes thick soon after the connectives have entered. The cephalic lateral portion of the ganglion is connected with the supraesophageal above by two large connectives, but smaller than those from the 1st thoracic ganglion. These cephalic connectives or crura cerebri are connected together a short distance away from the ganglion by a cross branch or commissure.

From the cephalic end there are three pairs of large nerve trunks, the *mandibular*, the *maxillary* and the *labial*. The *mandibular* is the largest the *labial* the smallest and most ventral. All appear to be mixed nerves, both sensory and motor. On either side of the middle line on the cephalic border are two small nerves, the *gustatory*, which are motor in part at least. On either side of the ganglion not far from its central portion is a small *ventral* nerve and not far from the connectives near the entrance of the caudal tracheal tubes are the small *salivary* nerves. I know nothing of the composition of these two last pairs.

The dense central mass of the ganglion prevents one from tracing nerve fibers very deeply in surface preparations, but a few more fortunate specimens gave now and then a fiber or a tract which could be easily followed. In general with the nerve trunks and connectives of other ganglia, these bundles of fibers entered the central portions and like them, too, the nerve cells were chiefly grouped on the sides with scattering cells on the dorsal and a denser mass on the ventral and caudal portions, but in this the dorsal side has more cells than was usual with the other ganglia. The same arrangement of cells and fibers was noticed as in others, that is, most of the peripheral cells could be seen to send their processes into the central portion. Fibers from the connectives above and below could be traced through the ganglion, but there were such masses of them that it was difficult to tell whether they were branched or not.

Fibers from the lower connectives were seen to end in the caudal portion of the "punksubstanz": (a) On the same side, (b) Crossing over the middle line. These were both superficial fibers and resembled those in the bases of the abdominal ganglia. Probably deeper fibers end higher up.

Fibers running *down* the upper connectives run: (a) Down the connective to end in the central portion of the ganglion; (b) Down the connective to end in the caudal region of the ganglion.

Probably among both of these groups of fibers there are some which cross over into the opposite side of the ganglion.

Fibers running down the connectives and crossing over to the opposite side through the commissure connecting the *crura cerebri*: (a) Cross over in the commissure to the opposite side and run down to end in the upper or lower portions of the ganglion.

Two other sorts may be given although no *complete* fibers were traced through such a course;

(b) It seems probable from the specimens that fibers cross to the opposite side in the commissure and run over to the opposite side of the ganglion:

(c) Probably some fibers cross in the commissure and run back to the brain.

Fibers running straight through the ganglion from above and from below were not traced but it is very possible that such are present as in other ganglia.

THE NERVE TRUNKS.

The mandibular branch sends its fibers into the cephalic dorsal border of the "punktsubstanz." Some of its fibers seem to end here, others pass in deeper.

The maxillary sends its fibers into the very center of the upper half of the ganglion and here some of them seem to end or cannot be traced farther in surface views. This is true of the more cephalic branch of the maxillary in part at least, while the rest of the fibers of this and those of the caudal branch are traced in laterally a little farther down.

The fibers of the labial nerve; some of them run in deeply about where the branch enters the ganglion, others go down farther and may be traced as far as the place where those of the ventral nerve trunk enter the mid-lateral portion of the central fibrous mass.

The salivary nerve fibers run in and can be traced to near the point where the ventral nerves were.

The small gustatory nerves run some distance down into the ganglion from the point where they take their exit and a motor nerve cell was found sending out its axon directly into this tract.

SUBESOPHAGEAL GANGLION STUDIED IN SECTION, BEGINNING AT THE CAUDAL END.

The connectives which run up to the subesophageal ganglion are much like the others described. As the caudal portion of the ganglion is reached these two longitudinal tracts of fibers become fused although they may be distinguished from each other. A group of nerve cells appears on the lateral sides, and a group of large ones on the median side dorsally, some of these

penetrate in between the tracts and a few cells appear ventrally on the median line, while the cells become more numerous laterally. The salivary nerves enter latero-ventrally and unite with the mass of longitudinal fibers. The cells disappear dorsally, but some are between the mass of fibers of each connective and the lateral cell group has become more ventral. There is at this level a transverse commissure on the dorsal side and fibers running down ventrally in the ventral line. Farther along the fibers do not so many of them run from dorsal to the ventral side and a median commissure comes to be formed. More cells come in laterally and ventrally and these sending their fibers into the central mass contribute to its complexity. These cells also run into the large but ill-defined median commissure.

Two little spots of darker more dense fibers come in on the ventral side and fibers from the ventral cells form an arch about them.

Farther cephalad the median commissure becomes less well defined. The dorsal is lost and a median group of cells comes in dorsally again. Fibers from the ventral and dorsal cells, especially the former go in curved sweeps to the dorsal and ventral sides of the fiber mass, fibers also run in laterally from the lateral cell groups. Farther along no clear commissure can be seen, but sweeps of fibers cross from both sides, those of opposite sides interdigitating to some degree. The ventral darker mass of fibers mentioned a short time ago has now become a transverse mass and is larger, being joined by fibers from the labial and ventral nerves. At the level of this entrance only a few scattering groups of cells are seen.

The dark fiber mass becomes expanded to the center of the "Punksubstanz."

The broad cerebral cruri are reached. From the central to the dorsal side laterally four small groups of nerve cells mostly small, with now and then a large one are seen. Fibers from the cerebral crus can be traced to the center of the fiber mass and into one or more of the several irregular masses of dark fibers. Dorsally and ventrally fibers cross from side to side and run diagonally from the dorsal to the ventral side. Farther along a ventral commissure of dark fibers is present, some of its strands reaching up into the dark fibers in the direction of the commissure and farther along breaking through it. A short dis-

tance cephalad of this point the ventral mass disappears and the lateral halves of the general mass of fibers becomes distinguishable once more as the upper region of the ganglion is reached. At this upper region, lateral cells are no longer seen, there is however, a small group ventrally placed, either side of the middle line and a small dorso-median mass. Fibers sent in from these curve up to run into the crus which may also at this level be seen to receive fibers from the middle and opposite parts of the ganglion by the way of a group of fibers just one side of the middle line and a group running from the center of the lateral central mass.

Just beyond this last level at the place where the maxillary branch enters, a little group of nerve cells comes in between it and the crus. Fibers from this large maxillary nerve run into the crus, into the central and ventral portion of the ganglion and apparently across to the other side, while many of its fibers are lost in the deeper staining central masses.

Farther along the ventral cells become much more abundant, a wedge shaped group 6-7 layers thick with a few large cells. A few cells come in on the mid-dorsal line and some come in latero-ventrally just above where the maxillary nerve joins the ganglion, and some of these cells seem to contribute directly to the nerve.

The large mandibular nerve joins the ganglion on its upper border, fibers come to it from ventral and dorsal sides of the ganglion and connections with the darker fiber masses in the center can be traced. Cells are now in masses both dorsally and ventrally as the cephalic end of the ganglion is approached and some of these at least seem to contribute directly to the nerve.

The above description is a very general one, only the main features of structure and arrangement were spoken of. The complexity of the ganglion is such that a general summary of it follows:

(a) *Cells*

The cells at various levels differ greatly. Beginning at the caudal end and passing forward there might be recognized about three main dorsal cell groups one after another which fuse and separate from each other at various levels. The median ventral cells are at first also separated from the other groups

but farther up they grow out laterally to become continuous with the lateral and dorsal cells at various levels while they become absent from the mid-ventral line, then become united again on the cephalic region where all the cell groups are joined together. In intervals where these groups are not in distinct masses a few scattered cells are often found.

(b) *Connectives*

Ventral connectives. Fibers from these run straight into the ganglion for a short distance until the central tangled mass is reached. Only a few of the fibers in the central part of the ganglion can be seen to take a straight course through it. Many others run straight or nearly so for a short distance and then turn off sharply to one side. Fibers from the connectives seem to end at all levels and in practically all parts of the central fibrous mass and to be contributed to by cell masses especially on the ventral side, but also clearly on the dorsal. These fibers coming in from both sides of the ganglion at different levels and as single fibers or groups add considerably to the complexity of the ganglion as does the fact that many of the fibers from the connectives which run through to the crura cerebri and nerves do not always take a straight course or run to the same parts of the nerve trunks. Sweeps of fibers for instance, can be traced quite straight up on the ventral side of the ganglion and then may be seen to turn over to the dorsal side.

Crura cerebri. These have fibers from the caudal connectives but not nearly all from them can be traced into the crura, for they are smaller and have their own special fibers which come from almost every part of the ganglion. The cells in various parts seem to furnish many of these, some of which come from the same side, but single strands were followed running in the direction of the crura which were from the opposite side. Fibers may also be seen to sweep back into it, probably from the mandibular trunk.

(c) *Nerve trunks.*

Mandibular. Many of the fibers of this end in the first part of the fiber mass. A few apparently run into the crura. Some fibers could be traced from near the median central part of the ganglion in a line with the lower connectives. Some came to it from cephalic median cells.

Maxillary. Fibers were followed into this from the lower connectives and from the upper parts of the ganglion. From this nerve trunk some fibers seem to end near the junction of the nerve with the central "punksubstanz."

Labial. This is made up from fibers which enter the ventral central portions of the ganglion, just above the entrance of the small ventral nerves. They may be traced from the connectives up and from the upper portion of the ganglion down into these trunks and ventral caudal cells evidently contribute fibers to the mingled mass which is connected with these branches.

(d) *Commissures.*

The commissures connecting the crura cerebri have fibers which cross from one side to the other in the case of descending or ascending strands. No other kinds were recognized although I think there is a strong probability that some fibers merely cross and do not descend at all.

Within the ganglion there are a number of commissures connecting the lateral halves. Some of these are of straight fibers, others are closely woven deep staining masses. Dorsal, ventral or median commissures are found at almost every level, especially ventral ones, although not always clearly marked. A longitudinal section through the whole ganglion shows from three to four main commissures, a cephalic, a caudal and two median ones.

THE SUPRAESOPHAGEAL GANGLION.

(Figs. 8, 9, and Pl. XVI, Figs. 1-4.)

The brain is made up of two large ovoid masses distinctly marked from each other on the middle line. It is connected on the ventral side to the subesophageal ganglion by means of the short, broad crura cerebri. All of the larger nerves come out laterally and of these there are three main trunks, the only ones to be considered at this time.

Three portions of the brain may be made out each connected with these trunks. The most dorsal is the *protocerebrum*, and it is also the largest and best marked and connected with the optic nerves which divide on each side into seven branches one for each ocellus.

The middle lobe of the brain or the *deutocerebrum* is the least marked of any and its nerve trunk the antennal, is the smallest of the three. It enervates muscles at the base of the antenna as well as sense organs in it and so is mixed. This lobe is best seen on the cephalic and dorsal side and not at all on the cephalic ventral.

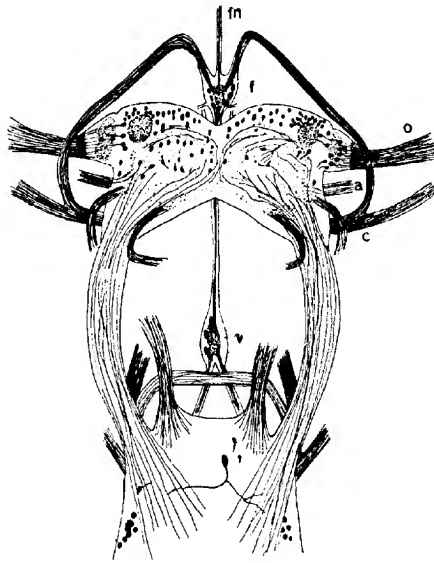


Fig. 8.

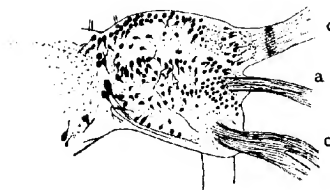


Fig. 9.

FIG. 8. Supra- and sub-esophageal ganglia with their attached nerves and ganglia. The brain is turned over cephalad. The sub-esophageal ganglion is dorsal. x30.

a.....antennal	fnfrontal nerve
c.....clypeolabral	v.....vagus ganglion
f.....frontal ganglion	o.....optic

FIG. 9. Cephalic view of one half of the brain. Methylene blue. x30.

Finally the *tritocerebrum* is well marked as a little lobe just dorsal of the crus giving off the rather large clypeo-labial trunk which with the arched nerve comes off as one. From the distribution of this it seems probable that it is mixed.

This arched nerve runs ventrally and cephalad to unite at the middle line with the one of the opposite side in the *frontal* nerve ganglion. A branch from this small nerve center runs forward as the *frontal* nerve, another runs back on the dorsal surface of the esophagus to the small *vagus ganglion*, which sends two branches farther down the alimentary canal.

General form of the Brain from Methylene blue.

In successfully stained preparations almost all parts of the brain, especially the parts in from the nerve trunks are seen to be covered with nerve cells, both large and small. Those just under the chitin seem to quite completely incase the central dark staining portions of the ganglion. This central dark mass in each well separated lateral half of the ganglion is roughly of the same general shape as the surface. In the main part out from the median portion there is a lobe deep in and opposite the ocular nerve, this is in the central portion of the ganglion and connected with it, but extending down into the tritocerebrum is another lobe almost as large near the crus.

Partly separated from the central lobe of "punktsubstanz" is a spherical mass of dark staining substance and out from this a little distance in the ocular lobe and beyond its constriction from the main part of the protocerebrum is another little mass of deeply colored material. About each of these last little masses of "punktsubstanz" a special arrangement of cells is seen, while over the surface of the main portion of dark substance on every side the cells form a thick covering.

Fibers running up the crura may be traced into the ganglion in its dorso-caudal region. Some apparently run only to the lower portion of the "punktsubstanz," others may be followed farther up and are lost in the central area. Fibers can also be traced to the central portion of the ganglion, to the medial portions and probably freely ramify all through the central mass.

Near the middle line of the ganglion some large cells on the surface were found with long processes extending down long distances in the direction of the crura and probably were continued into it.

The great bulk of fibers connected with the crura seem to take origin or terminate in the central portion of the "punktsubstanz."

The ocular nerves enter the protocerebrum through large nerve trunks which form a decided lobe on the surface of the brain. At the junction of this *ocular* lobe with the ganglion there is a little area of deeply staining substance mentioned, before and back of this are nerve cells, and also a few cells on the eye side of the mass. These may be seen to send their processes into a dark mass and in towards the main part of the brain. Fibers run out the nerve from the ocular lobes' deep staining mass and into the spherical body before mentioned and into parts of the "punktsubstanz" near it, the former are processes from cells located near the ocular "punktsubstanz." About the spherical mass may be seen many nerve cells whose fibers are connected with it.

Nerve cells on all surfaces of the protocerebrum are very numerous and may be seen sending their processes into the central fibrous mass of the ganglion.

The deutocerebrum is less marked than the other two neuromeres and the fibers of its nerve, the *antennal*, come in closer to the clypeolabial segment of the brain than the ocular portion. The fibers of the antennal nerve can be traced as a distinct band for nearly one-half of the distance from its entrance to the middle line, where they seem to end in a mass of deep staining fibers of the clypeolabral trunk where it joins the main central portion and here at least some fibers can be seen to end well towards the caudo-ventral portion of the ganglion.

The tritocerebrum is best marked in the dorso-cephalic side of the ganglion where it lies over the crus. The fibers of its nerve seem to be of two sorts. The labral part is often stained while the arched nerve portion is clear. Both branches enter the ganglion and plunge at once into the mass of deeply staining fibers. Not quite so many cells were stained overlying this region in the specimens prepared. Some of these sent fibers more or less directly into the central mass while others as in other surfaces of the brain seemed to be association cells in a small area.

SMALL GANGLIA OF THE HEAD.

Connected with the arched nerves somewhat cephalad of the brain is the frontal ganglion. This in well stained preparations may be seen to have a central deep staining mass surrounded by nerve cells, the processes of some of which run into the central mass, while those of others run out from the cell, and down into the nerve which runs under the brain and connects this with the smaller so-called *vagus* ganglion. This last is like the former only smaller and fewer cells surround the central mass, some of the fibers run from this and probably also rather directly from the cells of the ganglion, down and out the two caudal branches. Occasionally the two lateral ganglia of the esophagus take the stain but their connections or structure was not especially studied. They seemed to differ from the other two ganglia, as they showed from the surface no nerve cells, the whole body taking on a uniform deep blue color. Sections showed them composed of very many cells closely massed together.

Sections of the frontal ganglion show a small mass of cells quite well filling the caudal end, a few larger, but mostly smaller cells of the same general sort found in other places. Of these there were about two large and eight smaller ones at a level where the ventral nerves come off on each side of the "Punksubstanz," although farther cephalad than the place where these nerves are seen from the surface. Farther cephalad where there are only three or four large cells, fibers cross in various directions in the central portion of the ganglion. A large cell for instance was seen to send a process into the center of the ganglion where it broke up into a number of branches. Fibers cross in the various directions but most run longitudinally. At a level where a branch to the frontal ganglion arises, there are no nerve cells, the central part of the ganglion is divided into three masses of longitudinal fibers by trachea and cross fibers. This division is continued only for a short distance.

Farther along a dorsal and a few small ventral cells come in. The central mass of fibers is rather uniform, but made up of both cross and longitudinal strands. A little farther cephalad three cells come in dorsally at about the level where the arched nerves come off. Fibers running from side to side connect

these nerves through the center of the ganglion.

The so-called vagus ganglion has a central mass of fibers and its central part a nearly double row of cells closely packed about this central fibrous mass, these cells are continued down from the center a short distance, especially on the dorsal side.

THE BRAIN STUDIED IN SECTION.

(Plate XVI, Figs. 1-4.)

Only the main features of the structure of this complicated organ will be given at this time. Many of the elements of the brain of the adult may be present in the larva but for the proper interpretation of these it will be necessary to follow up this work with studies on the ganglia of pupae and adults.

As in the other centers, a central fibrous mass forms the bulk of the organ and about this central "Punktsubstanz" nerve cells are grouped in great numbers on practically all sides but the ventral. As in the other ganglia, large and small nerve cells and small neuroblasts are found, the latter are especially abundant and occur in great masses. Besides these, filling in between and in places where there are no nerve cells is the neuroglia network, which is often continued to the layer of surface supporting cells just under the chitinous sheath of the ganglion.

In sections we may recognize the dense staining parts seen in surface views to be masses of fibers more or less complexly arranged in the central and ventral portion, more or less paralleled by straight bands of the entering nerve trunks. Some of the special denser masses of fibers have already been described from surface views as that in the ocular lobe just as it joins the brain and in from the little spherical area just within and beyond this point. These two masses although quite separate from each other dorsally, ventrally and laterally are centrally connected by fibers and are also connected to each other to a less degree in the same way. The central fibers described in connection with the crura cerebri, are continued down into the labral lobe, but the deepest mass is in the central portion dorsally where it is somewhat lobed because of groups of cells on the surface and due to the processes of some of these cells passing down into the center. In this central "Punktsubstanz" either side of the middle line, is a well marked denser group of fibers, a rod of substance projecting from those on the

dorsal side of the brain. This runs down to the mid-ventral line and there branches into two parts, one ventral, the other dorso-lateral. Farther along each of these parts run caudally as a single piece, one ventrally, the other dorso-laterally and the middle portion of the rod and afterwards the dorsal part disappears in section because of the curve in it. Later the lateral part disappears and the mid-ventral portion extends in towards the middle line to meet, but not unite with its fellow of the opposite side, running caudally in this way some distance, just above a ventral fibrous commissure and below a broad central one. In other words this body is a long slightly curved rod standing up in the ganglion with its base divided into two portions of which the lateral is shorter, the median longer and extends in towards the middle line. These represent the *stalks* and *roots* of the "mushroom bodies," the cup, such as described by Kenyon and others is not present and the special cells if developed were not recognized. This stalk and root of fibrous substance seemed to have a lighter core, that is in sections it gave to some extent the appearance of a tube. The fibers which compose it are very densely massed together. Preparations in which the tissues were allowed to macerate showed them to be little affected.

On the cephalic margin of the brain as on the dorsal side, the central fibrous mass as a whole is lobed as already spoken of and masses of cells fill in over these. The cell groups are difficult to describe in detail. The whole dorsal and lateral portions of the ganglia are covered with them, both large and small and in places many cells deep. There are almost no cells on the ventral side of the brain.

Beginning laterally and dorsally we have about the spherical mass of fibers back from the ocular lobes, masses of cells, on the dorsal, ventral and mesal sides. A peculiar condition of some of the dorsal and ventral sides of this mass is the apparent epithelial character of some of the cells. Most of these are very small and are probably neuroblasts. The epithelial character is especially marked in two places on each side because there are little cavities one dorsal and one ventral in the outer portion of the circular mass of fibers. (Plate XV, Figs. 1, 2, 3.) There are some fibers from the two lateral groups of cells just described which run both to the mesal group and out the ocular nerve. This is also continued dorsally and forms all along

the dorsal part of the ganglion a thick layer, in the middle region of the brain.

A group of large cells occurs dorsally either side of the middle line, most of these point ventrally or centrally and send fibers to the crura cerebri, to the commissures and to the central portions of the fibrous mass; theirs are the longest fibers recognized from any cells in the brain.

Out laterally and ventral to the ocular lobes in the region of the antennal lobe and just above the crura is a small group of nerve cells, sending fibers into the crura and into the fibrous substance near that region of the brain.

In the cephalic region the cells surrounding the spherical mass may be seen divided into a dorsal, a ventral and a median group of small cells, already mentioned, while larger ones fill in on the dorsal side and are part of the general dorsal mass. These and the median masses run together and separate again at various levels, groups of smaller and larger cells often alternating, and these are continued on the cephalic and caudal sides of the ganglion. One of the most marked is a small group of cells surrounding a curved lobe of the central mass of the ganglion and continuous with cells on the cephalic side of the brain.

Fiber Tracts in the Brain.

(1) *The labial.* Fibers seem to end chiefly in the dense fibrous mass located in the labial lobe. A few fibers could be traced doubtfully into a dorso-lateral group of cells.

(2) *Antennal nerve.* Fibers from this end in cell groups either side of it. Fibers pass down ventrally into the lateral central part of the "punksubstanz" in large masses where some of them end, others cross to the ventral side and run in strands back in the main tract of the crura towards the other side. Others run towards the crus of the same side and apparently into it.

(3) *Ocular.* Fibers seem to end in the lateral mass of the ocular lobe, numbers of them connect this with the more median spherical "punksubstanz." Fibers connect these two masses and fibers from the surrounding cell groups run into one or both of them.

Fibers connect the ventral epithelial-like cell region with the lateral dark mass, and also with an adjoining group of small cells more medially situated.

The more median ventral mass of epithelial-like cells lying ventral to and slightly out from the spherical fibrous area probably has connections with the larger more dorsal cells.

The more dorsal of epithelial-like cells which are one side of a small cavity, send fibers into the lateral optic "punktsubstanz" and are connected by fibers with the more central dorsal cells which adjoin it.

(4) The *Crura cerebri*. The main mass of fibers goes up to the central portion of the "punktsubstanz" on each side and receives branches from all parts of it and also especially from the median and lateral dorsal cell groups and probably also from lateral masses. A large part of the band runs ventrally and forms or is joined into a commissure with fibers from the other side. Fibers come into this last from all ventral parts of the ganglion from *both* directions, from ventral parts of the mushroom bodies, and from various lobes of the deep staining mass of the ganglion.

(5) *Commissures*. Two commissures have been mentioned, a ventral which was described above. The other more medial is found toward the caudal region. It is short and broad.

SUMMARY.

1. In the abdominal ganglia practically all the nerve trunks and branches are mixed motor and sensory.

In the thoracic ganglia, the three main trunks are mixed. Pure sensory divisions were found in connection with cephalic branches. The branches given off between the thoracic ganglia and between the 1st thoracic and the subesophageal seem to be motor. At least the more caudal ones were determined to be, with fibers ascending and descending from the ganglia below and above.

The three large nerve trunks connected with the subesophageal ganglion seem to be mixed motor and sensory. The other smaller ones were not determined, but the small gustatory nerves were motor at least.

The three main trunks connected with the supraesophageal ganglion were all mixed but the ocular.

2. Sensory tracts were recognized entering thoracic and abdominal ganglia and distributed to various parts of the ganglion to which they were connected. That is distributed to one or both sides either as individual fibers or as branches from

ne. Some tracts were found distributed to the next center above as well as the nerve center to which their nerve trunks were connected. Others were found passing in to the ganglion to which the trunk was attached but giving no branches and passing on up to end in the next above or higher up.

A number of fibers apparently sensory were found passing through a number of ganglia without branches. These were often larger strands and although not traced as far as the head there was no reason to doubt that some of them were that long.

Sensory fibers and tracts were however traced into the large head ganglia and were found distributed to all portions of the fibrous mass. Sensory tracts were easily traced in connection with the ocular trunk, connecting it with the special lateral masses of fibrous substance.

3. Motor tracts could be traced as having their origin from cells in the ganglion to which the motor trunks were connected. Motor fibers could be traced out of the ganglia some distance but were not followed in as much detail as the sensory.

4. Association and descending tracts were recognized in all centers and at all levels of variable extent. Probably some of these were motor tracts.

5. Cells of many sizes were found in all centers. The largest and the smallest functional nerve cells seemed to be for association, those of the former sort having extensive arborizations, the second kind being much less extensively branched. Many of the medium sized cells were found to be motor. The general type was uni- or bipolar with one long branch which might run out for a considerable distance. Some association cells seemed to be bipolar with long processes running out in both directions. Some association cells seemed to be uni- or bipolar with all the branches coming off and branching again not far from the cell. A few multipolar forms were seen.

Neuroblasts were found to some extent in all ganglia, but great masses of them were especially noticeable in the brain.

Neuroglia networks filled in places under the chitin where there were no nerve cells and also formed more or less of a network in the regions where they were present.

6. Cells were grouped about the central fibrous mass in all of the ganglia. In the abdominal they were found to be especially abundant in the caudal and ventral regions, although the cell masses extended out laterally in all, and there were

often well marked mid-dorsal masses of large and smaller cells as well as scattered cells in all parts. In the more cephalic ganglia, the cells are not quite the same in distribution. Cell groups and masses are found abundantly ventrally, but also on the dorsal and lateral sides and also great masses of them at the cephalic as well as the caudal end.

In the supra esophageal ganglion, cells are especially abundant dorsally and on the cephalic and caudal borders, less abundant laterally and ventrally. The cells are very numerous. Each side of the middle line a group was located with very long processes, the cells being mostly large.

Other groups were densely massed lateral to these, both cephalad and caudally, some of them were large, others small, and two groups of small cells on each side out near the optic nerves were found with a cavity near them.

Nerve cells were found partly surrounding two masses of fibers on each side near the optic nerves.

From the distribution of the cells and fibers there was no evidence of the dorsal cells being especially *motor* and of a ventral, particularly *sensory* region as Binet was led to think from experiments. I would rather incline to Kenyon's idea of ventral motor and dorsal sensory if I choose either of the two views, as undoubtedly most of the ventral cells in the thoracic and abdominal ganglia are motor cells, while many if not most of the fewer dorsal cells of these ganglia seem to be association cells, sending their fibers superficially over the surface or deeply into and *through* the fibrous mass to be associated with the cells and fibers of the ventral side.

7. In all of the ganglia the central mass into which many of the nerve cells send their processes has a very complex arrangement of fibers and nerve terminations. Certain portions of this mass in all are much denser than the rest.

In the brain this central "punktsubstanz" is somewhat more intricate in its texture on the dorsal side than on the ventral and is more or less lobed while off from the central mass there are two smaller groups of "punktsubstanz" in connection with the optic nerves on each side. In the central part of the brain is a *stalk* and *root* of a mushroom body on either side, but the *cup* is not present. The ventral portion of the ganglion is mostly made up of *straight fibers*.

In all of the lower ganglia there are at almost any level, from one to three commissures recognizable, a dorsal, a median

and a ventral. These are broken up at various levels so that there may be several, three or more, cephalic or caudal parts of these commissures. There are more in the 8th abdominal and in the subesophageal than in the others.

From dorsal to ventral sides also, fibers chiefly from dorsal cells connect the upper and lower surfaces.

In the brain there are two commissures a broad short median and a longer ventral. Many other cross and longitudinal fibers connect all levels.

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PLATE XV.

A series of four photographs of cross sections through the 1st thoracic ganglion of *Corydalis* through a caudal level. The last figure is through the more central portion of the ganglion. Nerve cells show at the sides. The central fibrous mass is shown in all, and longitudinal fibers can be traced. In the last three figures cross commissures may be seen. The dark mass at the left or ventral side is part of the surrounding tissues and not a part of the ganglion. x60.

PLATE XVI.

FIG. 1. Photograph of a cross section parallel with the long axis of the brain through its central region. One half only shown. The dorsal side is up. The optic nerve is the swelling off at the right above, while leading off below is the broad crus. The dorsal masses of cells show, also central fibers and the stalk and root of the mushroom body. x75.

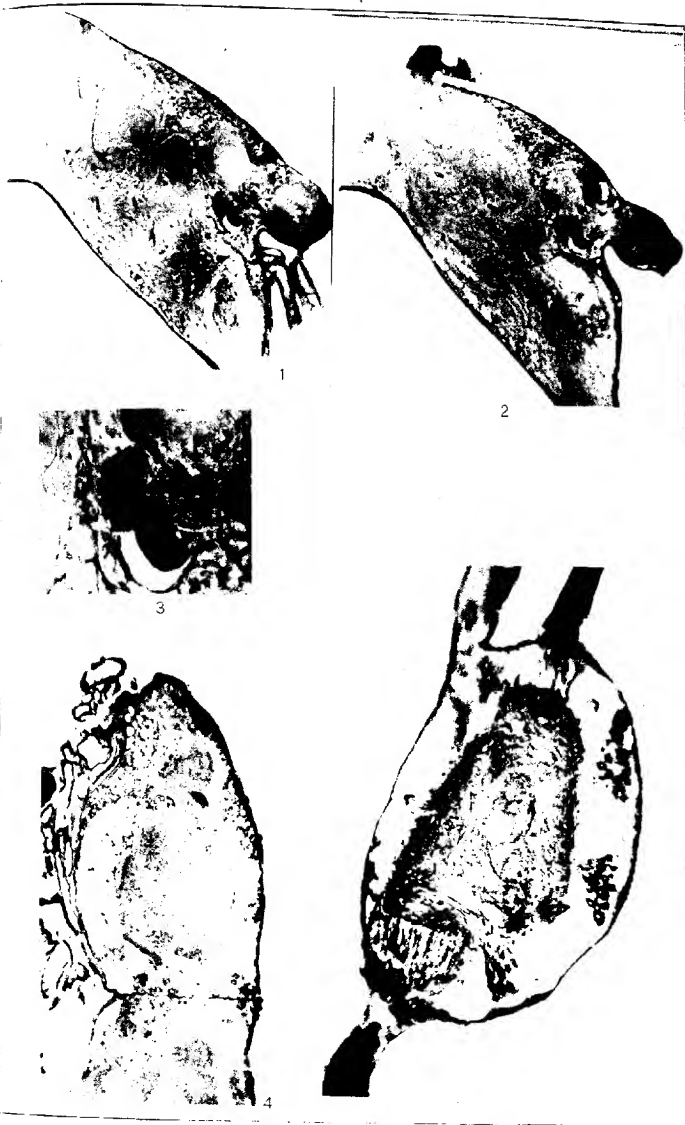
FIG. 2. A similar photograph from the same series cut farther one side, cephalad. x75.

FIG. 3. Photographs of the larger cavity shown in Figs. 1 and 2. x250.

FIG. 4. Section of the brain cut in a similar way as Figs. 1 and 2, but farther cephalad. The ventral side is at the left. The dorsal to the right. x75.

FIG. 5. Longitudinal section of the sub-esophageal ganglion. Above the first branch to the left is one of the crura cerebri, the next it is the mandibular. Below the branch cut only through its edge is one of the ventral connectives. x75.





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STRUCTURAL STUDY OF THE CATERpillARS.— II. THE SPHINGIDAE.

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This paper may be considered a continuation of that published in the ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA, III, 94-132, with plates 10 to 20. The references to figures with the prefixed numeral I, refer to plates 13 and 14 of that article.

In the caterpillar stage the SPHINGIDAE may be defined as follows: With secondary hair on the body, epicrania, front, clypeus, maxillae and labium, but never on the antennae or distal parts of the maxillae and labium. There is almost always secondary hair on the adfrontals. It is present on the mandibles in *Cressonia* only, and the labrum bears a single additional hair in *Pachysphinx*. Front not more than half the height of the head (measuring here and elsewhere in this paper from the base of the front to the vertex. The frontal punctures are close together, and when distinct the primary setae are somewhat further from them than they are from each other, but they are distant from the outer edge of the front. The lobes at the two lower outer angles of the front tend to be large. Adfrontals not very wide, often narrow, not extending between the clypeus and mandible when distinct in the lower part; puncture a little below the upper seta. Clypeus narrow in the middle, often grading into the membrane below. Labrum well marked, often with very deep notch; vi distant from the margin, and usually directly below ii. Mandible with a large scrobe, bearing the two usual setae, one at the tip, and the other about half way out, toward the posterior side. Antennae with second joint most often twice as long as the first; the remaining joints exceptionally minute. Maxillary palpi stout, the second joint somewhat shorter than the first; submentum ill-defined, and mentum broad at the base. Spinneret broad, flat and short, with the usual three sclerites; labial palpi similar in form, and set obliquely to it, forming with it a sort of scoop (which would seem more useful in feeding than in spinning).

Claws not distinctly notched, broadening abruptly at their base. Prolegs with a double row of hooks, about 20 to 60 in number; not very regularly arranged in *Hemaris*, etc. The hair on the prolegs is never as rudimentary as higher on the body.

Secondary hair always minute, rudimentary, mostly visible only under a lens; but the body is often roughened by the tubercles; primary hair (iii and v alone are easy to identify but in *Proserpinus flavofasciata* i and ii are marked by larger black spots) often considerably better developed; but their tubercles are never raised, even when the others are. Segments with 8 or 9 annulets, usually ill-defined in front. Usually with a wart, horn or peculiar marking on the dorsum of the eighth abdominal segment—if a horn, bearing tubercles and secondary hair. With other armature only in *Ceratonia amyntor*, *Lintneria eremitus* and some exotic *Smerinthinae*.

Tree-feeders with a few exceptions (*L. eremitus*, *Deilephila*, *Protoparce*, *Choerocampa*) or feeders on vines.

In synoptic form the Sphingidae are distinguished as follows:

1. Maxillary palpi three-jointed; the four upper ocelli in a rectangle; the upper setae of thoracic segments on a level. **JUGATAE**
1. Maxillary palpi with but two free joints; the four upper ocelli in a curve; the upper setae of the thorax, when single, one above the other. **(FRENATAE)**
2. With outer hooks on the prolegs. **Microlepidoptera**, etc., etc.
2. With a single inner band of hooks on the prolegs. **3**
3. Hooks of prolegs alternately of three lengths. **Butterflies**
3. Hooks of prolegs all of the same length. **Noctulidæ, Notodontidæ, Arctidæ, Eucleidæ, etc.**
3. Hooks of prolegs alternately and regularly of two lengths. **4**
4. Secondary hair present on antennæ and palpi. **Lasiolepidæ**
4. No secondary hair on antennæ or palpi. **5**
5. Secondary hair if present, confined to leg-bases. **Geometridæ, Thyatiridæ**
5. With dense secondary hair on body and head, including labrum. **Apatelodes (Eupterotidæ ?)**
5. With considerable secondary hair on body and head, but little or none on labrum. **6**
6. Primary tubercles represented by branching spines, or warts bearing several hairs. **Saturnioidea**
6. Primary tubercles bearing minute simple hairs, hardly distinguishable from the secondaries; and all hair minute. **SPHINGIDAE**

SEMANOPHORÆ and **ASEMANOPHORÆ** are separated rather by different tendencies than by sharp differentiating characters, and the same is true to an even greater extent of the subfamilies of each. Marking in a general way the *Asemanophoræ* there may be mentioned the strong tendency for the head to taper toward the vertex (which none of the *Semanophoræ* show); the densely granulated skin of the middle stages (except *Lapara*, and shared by one or two *Semanophoræ*); the generally higher front, with more tendency to develop lobes at the lower outer angles. The first abdominal segment is never swollen, and the horn is never replaced by an eyespot; the clypeus tends to be wider, at least at the ends.

In the majority of the *Semanophoræ* the last thoracic or first abdominal segment is much swollen, and the horn is frequently replaced by an eyespot. The front often makes a perfect equilateral triangle. The skin is very sparsely if at all granulated in the last stage, and is rarely granulated in the earlier stages. On the labrum, seta iii is quite generally on a level with ii, in the *Semanophoræ* more often nearer the level of vi, at least in normally formed labra. Normal oblique stripes are rather rare.

If we except *Pachysphinx occidentalis* we might define the SMERINTHINAE as caterpillars with heavily granulated body in the last stage, and more or less granulated head, with the setæ rising from the apex of the granulations. All except *Pachysphinx* have an acute triangular head, and even in this the head tapers strongly toward the vertex. The labrum is always normal in arrangement of its setæ, with the distance between the setæ ii full half the width of the labrum, and with moderate, flaring notch. Except in its smooth skin, and normal horn *Pachysphinx occidentalis* agrees exactly with *P. modesta*, and in horn it agrees with *Smerinthus*.

The SPHINGINAE, which comprise the rest of the *Asemanophoræ*, are less homogeneous. *Ceratomia* has a densely granulated skin, but is distinguished from all the *Smerinthinae* by possessing a row of middorsal granulations. In the more specialized forms the labral setæ are closer together around the notch, and this reaches its extreme in *Cocytius*, which has a head of normal *Smerinthid* form. *Lapara*, also with a triangular head, is easily separated from the *Smerinthinae* and placed in this series, as its labrum (as well as markings and habits) agrees closely with *Hyloicus*.

I cannot distinguish the three subfamilies of *Semanophoræ*, even by tendencies, and am inclined to treat them as a single subfamily. The eyespot in place of a horn occurs only in the *Philampelinæ*, but they are not all of the same type. Humped caterpillars occur in all three (*Choerocampa*, *Darapsa*, etc., *Erynnis*) and cylindrical ones also (*Deilephila*, *Sphecodina*, *Pseudosphinx*); reduced horns (*Pergesa*, *Pholus vitis*, and *Erynnis*) and normal ones (*Xylophanes*, *Darapsa*, *Hemaris*); rounded heads (*Deilephila*, *Macroglossa*, *Pseudosphinx*) and squarish ones (*Choerocampa*, *Darapsa*, *Erynnis*). The labrum of *Pseudosphinx* and *Erynnis* is a little peculiar, but that of

Deilephila comes as near as that of Hemaris, to it. *Hemaris croatica* is an almost perfect connecting link between *Hemaris* and *Macroglossa*. Altogether a tabulation of the genera which shall be workable must be mainly artificial in its arrangement.

THE GENERA (AND SUBGENERA) OF SPHINGIDAE.

1. Head high and triangular, no horn..... *Lacera*
1. Head rounded, or horn more or less developed..... 2
2. Head half higher than wide, horn well defined, enlarged tubercles on anal plate..... 3
2. Otherwise..... 4
3. Four tubercles on anal plate, face smooth..... (*Dilina*)*
3. Two tubercles on anal plate, face rough..... *Cressonia*
4. Head much higher than wide and triangular; horn rather small and soft, not well distinguished from the body..... 5
4. Head about as wide as high, or trapezoidal..... 6
5. Face smooth, sides tuberculate..... (*Amorpha*)
5. Face as rough as sides of head, all heavily tuberculate..... *Smerinthus* and *Paonias*
6. Seven setæ on labrum, transverse ridges,—one each on meso- and meta-thorax..... *Pachysphinx*
6. Six setæ on labrum, transverse ridges more numerous or wanting..... 7
7. Body heavily granular, with granular obliques, middorsal line, and subdorsal on thorax, the latter raised into two pair of short horns..... *Ceratomia*
7. Body smooth or nearly so in last stage, no middorsal granules..... 8
8. Labrum with ii decidedly higher than i..... *Hyolocus* (*cupressi*?)
8. Labrum with ii on a level with i or lower..... 9
9. Head triangular, smooth, as well as cervical shield; anal plates exceptionally rough; labrum with a deep narrow notch, with the setæ i, ii and vi crowded around it..... *Cocytus*
9. Head rounded on the vertex, but in *Chlænogramma* with two enlarged granulations; anal plate rarely rough; setæ ii of labrum almost half as far apart as width of labrum, or more..... 10
10. Head much higher than wide, and tapering to about half its width at the vertex..... 11
10. Head as wide as high; tapering decidedly toward the vertex..... 12
10. Head nearly as wide as high, rounded or squarish, or if tapering a little then strongly granulated..... 17
11. Horn nearly twice as long as height of head..... *Chlænogramma*
11. Horn slender, and but little longer than height of head..... *Daremma* (*undulosal*)
12. Horn recurved at tip..... (*Acherontia*)
12. Horn regularly pointed..... 13
13. Notch very shallow, in depth only 1-7 height of labrum..... *Phlegethontius*
13. Notch of labrum at least twice as deep..... 14
14. Horn very slender, head well rounded at the sides..... *Daremma* (*catalpæ*)
14. Horn normal or short..... 15
15. Mesothorax acutely humped, sometimes surmounted with a tubercle..... *Lintneria*
15. Body normal in form..... 16
16. Head normally with two pair of back side-stripes..... *Herse*
16. Head normally with one pair of dark side-stripes..... *Sphinx*
17. Head heavily granulated, body cylindrical, with normal obliques on sides..... 18
17. Head not granulated, or body swollen, or without oblique stripes but with a continuous subdorsal picked out in enlarged granulations..... 19
18. Body somewhat granulated in last stage, especially on the obliques, etc..... *Atreides*
18. Body unusually smooth..... *Dolba*

* Exotic genera in parenthesis.

19. Setae i, ii and iii of the labrum on a level; labral notch very shallow, abdomen cylindrical and rather slender. 20
19. Setae i higher than ii and iii, ii usually decidedly higher than iii. 21
20. Metathorax swollen, supraanal not noticeably armed. *Erynnis*
20. Cylindrical, supraanal with two large tubercles. *Pseudosphinx*
21. Horn reduced to a granule or replaced by an eyespot; metathorax strongly swollen; head full as wide as high and squarish. *Pholus*
21. Horn present in all forms with swollen body, swelling rather belonging to the first segment of the abdomen than to the thorax; head rounded, or if squarish, full as high as wide. 22
22. Horn wanting. (*Deilephila vespertilio*)
22. Horn replaced by an eyespot. 23
22. Horn conical well developed. 24
23. Head very rough in last stage, horn very slender in middle stages, replaced by a high tubercle in the next to last. *Sphæcodina*
23. Head nearly smooth in the last stage; horn stout in penultimate.
24. Horn blunt and cylindrical; body marked with a large subdorsal eyespot on the thorax, and with well defined distant annulations, beginning with the second abdominal segment. (*Daphnis*)
24. Horn acute; no eyespot on side of thorax. 25
26. Body more or less swollen on first segment of abdomen, thence tapering to the head. 30
25. Body not swollen. 26
26. Head and general surface of body distinctly but sparsely tuberculate, the setae rising from the apex of the tubercles; cervical and anal shields rougher than the rest of the body. 27
26. Body smooth, head rarely with very slight tubercles, from the slope of which the setae rise. 28
27. Tubercles only visible under a lens. (*Macroglossa*)
27. Head and cervical shield appearing rough to the naked eye. *Hemaris*
28. Notch of labrum hardly 1-3 its height; setae i and ii spaced about in the ratio 2:3; vi only 1-3 way up from the apex of the lobe toward ii and much nearer the middle line. *Deilephila*
28. Notch of labrum deeper, setae i and ii only about half as far apart as the setae ii are from each other; vi nearer to ii than to the apex of the lobes. 29
29. Front about half as high as height of epicrania; without normal oblique stripes (with reversed oblique spots). *Proserpinus* (in part)
29. Front smaller; with seven normal obliques. 14
30. Horn not so long as height of head. 31
30. Horn very slender. (*Hippotion*)
30. Horn normal. 32
31. Head very finely granular, appearing under low power smooth and dull. (*Pergesa*)
31. Head distinctly vermiculate. *Amphion*
32. Head sparsely tuberculate. 33
32. Head smooth and dull under low power, granular under high power, with smooth areas about the setae. 34
33. Body slightly swollen, spiracles pale with two black bars. *Deidamia*
33. Body much swollen, spiracles dark with a white dot at each end.
34. Front higher than wide. *Darapsa*, *Ampeloeca*, (*Clarina*)
34. Front wider than high. (*Theretra*)
Xylophanes

Sphinx. (*Hyloicus* in part). Head slightly tapering toward the top, or with sides rounded out (*S. drupiferarum*), with irregular vermiculate grooving; the setae rising as often from the grooves as from the elevated portions. Front about $\frac{1}{3}$ height of head, with lobes at the lower outer angles well marked

and about $\frac{1}{4}$ to $\frac{1}{3}$ its height. Ends of clypeus as wide as $\frac{1}{2}$ height of front. Labrum high, with a notch $\frac{1}{4}$ to its width, the setae i and ii spaced about in the ratio 1:2, vi a little nearer in *S. drupiferarum*, a little farther off in *S. gordius*, *luscitiosa* and *eremitus*; iii, a little higher than vi but much below ii; notch deep and slit-like in *S. gordius* and *luscitiosa*, shallower and more flaring in the others. Mandible with few (perhaps four, but ill defined) large teeth. Second joint of antenna decidedly longer than the first, and nearly twice as long as wide. First segment of body much larger in diameter than head and more or less enclosing the back of it. Skin entirely smooth, granulated until the last stage; supraanal more or less granulated. Horn normal, much longer than head, and curved downward. The seven stripes similar.

There is also some variation in the horn. In the majority of species it is cylindrical in the basal part, and strongly down-curved in its entire length; but in *chersis* the basal part is more often nearly straight, and in *gordius* it is regularly conical and the whole horn is almost straight. The European species *ligustri*, which comes next to *drupiferarum* in the adult, in the caterpillar resembles it closely in markings, but has the normal Sphinx head. (Fig. 1). That of *drupiferarum* would not differ in face view from Fig. 10. See also I, Figs. 39-41 of *S. gordius*.

Lintneria has a conical hump on the mesothorax, which in the next to last stage, and sometimes in the last, is surmounted with a hard tubercle. Otherwise it resembles Sphinx in structure. It is considered a subgenus of Sphinx. (*L. eremitus*, Fig. 8.)

Ilyloicus. Head rounded and decidedly larger in diameter than the body. Horn straight and slender. Labrum with very shallow widely flaring notch; with setae i and ii nearly evenly spaced; ii much lower than i and the setae i, ii and vi of each side forming an equilateral triangle. Second joint of antennae only half longer than wide, and first joint very short. Supraanal long and triangular. Fig. 10.

H. pinastri is longitudinally striped with green and white, with a broad red dorsal, or else suffused with red. Horn black. *H. cupressi* of the southern states is reported as similar, with the white lateral stripes broken into patches; and is probably similar in structure.

Herse. I cannot distinguish *Herse* from *Sphinx* by any satisfactory characters. The head in both *convolvuli* and *cingulata* is intermediate between those of *drupiferarum* and the other *Sphinxes*. Setae i and ii of the labrum are about $\frac{2}{3}$ as far apart as the distance between the two setae i, and i is but little higher than ii. The two main joints of the antennæ are practically equal. In the only specimen of *H. cingulata* I have seen the horn is very short, but this may be an abnormality; it is normal in *H. convolvuli*.

Dolba. The head does not taper decidedly toward the top, and is decidedly granular, the setæ rising from the apex of the widely separated granules, as in *Smerinthus*. Otherwise it agrees with those species of *Sphinx* in which the labrum is not deeply notched. The head comes surprisingly close to that of *Darapsa*, but may be distinguished by the decidedly higher front, and the fact that iii of the labrum, as in most *Asemanophoræ*, is nearer to the level of vi than ii. I, Figs. 39-41 represent not this species but *Sphinx gordius*.

Atreides has a very similar head. The supraanal plate is an equilateral triangle; the markings are picked out with raised granules, and there are several transverse rows on the thorax, and scattered granules on the abdomen as in *Smerinthus*, but very widely scattered and small.

Acherontia. Has a slight transverse hump on the mesothorax (suggested in some *Sphinx*); the tip of the horn is recurved sharply; the fine annulations are wanting from the thorax. Otherwise entirely like *Sphinx* (e. g. *S. kalmiae*). *A. atropos* examined, European.

Ceratomia. (sens. str.) Head about as wide as high, decidedly tapering, somewhat granulated in back, but with the setæ not springing from the granulations, structurally as in the lower species of *Sphinx*. Body densely granulated, with the subdorsal and obliques picked out in raised granulations, and also with a *mid-dorsal row*. The subdorsal row is produced on the meso-, and metathorax into two pairs of short soft horns. (I, Figs. 45 and 49.) Aside from subfamily characters, I have seen no trace of kinship between this species and *Daremma*. The latter seems to come closer to *Chlaenogramma*.

Daremma. Skin smooth; horn normal, rather slender and short; or longer but very slender (*catalpæ*). Head slightly granular, but the setae do not rise from the apex of the gran-

ulations. Otherwise the characters common to *undulosa* and *catalpæ* are shared by *Sphinx*.

In *D. undulosa*, the type, the head is $\frac{1}{2}$ higher than wide, very strongly tapering toward the vertex, the horn is only a little slenderer than normal, and the labrum is moderately notched, with seta iii in the normal place. In *D. catalpæ* (Fig. 11), the head is broad and rounded, shaped as in *Deilephila*; the labrum is quite deeply notched, with iii nearly on a level with ii, as in the *Semanophoræ*; the body is unusually cylindrical and the horn is very slender. I have seen a specimen from the U. S. National Museum, with no data but the name *Daremma hageni*. It is a typical *Smerinthus* in structure, and could be the fourth stage of one of the larger species (*cerisyi*), but is rather sparsely granulated. I should suspect it was misidentified.

Chlænogramma. Head like that of *Daremma undulosa*, but with inconspicuous enlarged granules on the vertices. Body like *Atreides plebius*. Horn normal in length.

Cocytius (antæus). Head not at all tuberculate, but decidedly higher than wide, and terminating in two enlarged granules, like a fourth-stage *Smerinthus*, but higher and closer together at the vertex. Front full as high as wide, the lobes at the outer lower angles are not only well marked in outline, but project very conspicuously; front less than $\frac{1}{2}$ height of epicrania, iii and ii of the labrum are on a level, but the notch runs even higher, and is very narrow. The distance between the two setæ ii is less than $\frac{1}{2}$ the width of the labrum, and i, ii and vi are all located practically in the notch. Cervical shield as smooth as head, the anal is very rough, like the horn, and is a narrow triangle. Skin not at all granulated. Altogether an unusually distinct genus for this series. The structure so far as it is not unique suggests *Sphinx* rather than any other genus, but I understand the moth comes nearer to *Phlegethontius*.

Phlegethontius (Protoparce) Notch of labrum only one-seventh its height, not reaching the level of seta vi; iii and iv not so high as usual. Caterpillar distinctive in appearance, but not otherwise separated in structure from normal *Sphinx*. *S. rusticus* is said to be sparsely granulated on the lines. 1. Fig. 51.

Lapara (Ellema). Skin quite smooth, not only in the last, but in earlier stages. Horn wanting entirely. Anal plate full as long as wide and acute. Head somewhat higher than wide. (Fig. 4), in the earlier stages extremely high, triangular, with small and distant tubercles, like Fig. 12; front $\frac{1}{3}$ its height, higher than wide. Labrum (Fig. 5) with a very shallow notch, broadly flaring, with the apex of the lobes far to one side and the outer edges nearly straight; i lower than ii, but not so much so as in *Hyloides*, i and ii about equally spaced; both crowded down toward the margin; vi decidedly nearer the middle line than ii. Scrobe of mandibles smaller than usual. Second joint of antenna hardly longer than wide, and first joint very short. First ocellus directly behind the second, and nearer to the posterior one than the second is to the fourth. With longitudinal stripes, or checkered, never with obliques.

Except for the labrum and markings, which are essentially as in *Hyloicus pinastri*, there is nothing to connect this genus with the *Sphinginae* in the caterpillar; there are a couple of parallelisms to the *Smerinthinae*; the shape of the head, and low first ocellus as in *Cressonia*.

I cannot distinguish the species in the caterpillar.

Smerinthus (Sphinx) and *Paonias (Calasymbolus)* (I, Figs. 12-14). Head decidedly higher than wide, triangular; with nearly acute apex and sides somewhat rounded out; with numerous widely spaced raised tubercles, each bearing a seta; front about as in *Sphinx*, with several tubercles somewhat smaller than those on the epicrania; labrum with a notch about $\frac{1}{4}$ its width, in depth, with the setae arranged as in *Sphinx*, but the distance between the two setae vi is full half the width of the labrum (in the *Sphinginae* it is mostly distinctly less than half); iii, iv and v about equally spaced on the outer edge. Clypeus and mandible and antennae as in *Sphinx*, but the adfrontals are somewhat wider. Body finely granulated, strongly tapering toward the head; first prolegs less used than the others and slightly reduced. Subdorsals on thorax, and obliques on abdomen marked by rows of raised granules. No granules on the middorsal line, but they show a tendency to arrange themselves in a row on each side of it. Horn soft, not well distinguished from the body and about as long as the height of the head, not down-curved. Supraanal an

equilateral triangle in shape, not specially armed, acute. The transverse rows of granulations on the thorax are all about equal. Ocelli in normal arrangement, as in *Sphinx*.

The species show very little distinctive in the way of structure (or for that matter in color and markings) *P. (Calas m. bolus) astylus* may be a little rougher, with better developed setæ than the others, both on head and body, and the horn seems a little better defined in *S. ocellatus* than the others.

Pachysphinx (*Triptogon*, *Marumba*). Head wider than high, with sparse granulation on the sides, nearly smooth, but a little vermiculate on the face; the apex bluntly rounded. No subdorsal row of granulations on the thorax but the meso- and meta-thorax each have one high transverse crest. Horn soft, variable in size. The three lower ocelli form a right triangle, the posterior being unusually high. The labrum has an additional seta, on the margin; the four marginal setæ that result are about equally spaced.

1. *P. modesta*. Body normally granulated; about as in *Smerinthus*; horn minute, about $\frac{1}{8}$ in. long; thoracic crests high and granular. (Fig. 7.)

2. *P. occidentalis*. Body smooth, with a few raised granules on the last oblique line, only; horn about as long as height of head. Thoracic crests rounded over and hardly distinguishable. (In the penultimate stage it is granular like *P. modesta*.) This, as may be seen, is very different from the eastern form *modesta*. (Bred from the egg by Mr. Brehme; Western.)

Amorpha (*A. populi* of Europe) Labrum very deeply notched (like *Cressonia*). Head decidedly higher than wide, triangular, smooth on the face. Anal plate unarmed, and horn, etc., as in *Smerinthus*. The last four oblique rows of granules very distinctly extend over three segments. The characters are nicely intermediate between *Smerinthus* and *Dilina*, showing no special closeness to *Pachysphinx*.

Dilina (*Mimas*). Horn sharply separated from the body and down curved as in *Sphinx*; half longer than width of head, mostly cylindrical. With a longitudinal subdorsal row of granules on the thorax. Head half higher than wide, and acute-triangular. Face smooth, the sides of the head sparsely tuberculate. Supraanal with four raised tubercles in a rectangle. Otherwise about as in *Smerinthus*. *D. tiliae* of Europe.

Pressonia. With only one large pair of enlarged tubercles on the supraanal plate. Front as wide as high and only one-fourth as high as the epicrania. Entire head tuberculate; first ocellus moved down and posterior one up so that they are not so far apart and as the second and fourth are from each other. *Mandibles with a tuft of secondary hair* on the outer part of the serration. Otherwise as in *Dilina*. *C. juglandis*. (Figs. 12 and 13.)

Deilephila (*Celerio*) (Fig. 9, and I, Figs. 46 and 52). Head distinctly wider than high, rounded on top, roughened with irregular grooves, but not as strikingly as is usual in the *Sphinginae*. Front triangular, the outer edge but little sinuous; clypeus narrower at the two ends than in the *Sphinginae*. Labrum with a broadly flaring notch only one-third as deep as the height of the labrum or less, setae i and ii about two-thirds as far apart as the setae i are from each other, nearly on a level; vi less than half way up to ii. Antenna with the first and second joints nearly equal in length and diameter. Ocelli with the first four of nearly equal size, in a regular curve, but the second decidedly nearer to the third than to the first. Posterior ocellus about half way between the upper and the lower; the three lower ocelli forming approximately a right triangle. Skin smooth, the tubercles marked by tiny chitinous rings, those of the primaries two or three times as large as the others. Horn normal, moderate, entirely wanting in *D. respertilio*. Supraanal broad. Caterpillar as a whole cylindrical, tapering toward the head, almost always with a conspicuous row of subdorsal spots or eyespots, which are all about equal in size except the last. The front is smallest in *D. euphorbiae*.

D. lineata, *gallii*, *euphorbiae*, *lathyri* and *respertilio* were examined. Aside from those mentioned above the differences come down to a slight variation in the depth of the notch of the labrum; and the markings.

Cherocampa (in the broader sense). (Fig. 6.) Head squarish, full as high as wide, very finely granular, so as to appear smooth and dull with low power; the region about the setae may be glossy but not raised. Front triangular, wider than high (except in *alecto*) at least $\frac{2}{3}$ height of head; posterior ocellus lower making the triangle formed by the three lower ocelli acute-angled; second joint of antenna about twice as long as first; notch of labrum at least $\frac{1}{3}$ its height, usually more; i

and ii only half as far apart as the two setæ i are from each other; vi nearer to ii than to the tip of the lobes. Body with the first abdominal segment much swollen and bearing an eyespot, with or without less prominent ones on the following segments; thorax lacking the mottling characteristic of the abdomen in the darker forms; horn regularly conical; skin smooth.

Subgenus *Theretra*. Horn well developed; large eyespot normal, followed by a series of simpler ones in a subdorsal stripe; pattern of abdomen wanting from the first segment, as in some *Philampelina*; body with dark obliques slanting up and back. *T. alecto*.

Subgenus *Xylophanes*. Horn and eyespots as in *Theretra*, front distinctly wider than high; labral setae i and ii a trace farther apart and nearly on a level; notch broad and only $\frac{1}{2}$ height of labrum; second joint of antenna only half longer than the first. Perhaps a little near to *Deilephila* than the others are. *X. tersa*.

Subgenus *Pergesa*. Horn very short and sharply down-curved; the first eyespot only is present, and it has a black shade below. Setae i of labrum much higher than ii, and they are spaced as in *Theretra*, that is, in the ratio 1:2. Notch nearly half height of labrum; antennæ with second segment twice as long as first.

Subgenus *Hippotion*. Similar to *Pergesa*, but with the horn long and slender (fig. 15).

Pholus (*Philampelus*). Horn reduced to the merest rudiment in *vitis*, replaced by an eyespot which bears a pale crescent in its posterior part, in *pandorus*, *achemon* and *labrusca* said to be completely wanting in a Texan species. Metathorax much swollen, first segment of abdomen distinctly smaller. The front of the body is completely retractile in *P. achemon* and *pandorus*, apparently less so in *vitis* and *labruscae*. Supra-anal broad, not specially armed. Head fully as wide as high, squarish; front higher than wide, and nearly half its height. Setae i, ii and vi of labrum especially close together.

Ampeloeca. (*Darapsa*, *Everyx*, *Ampelophaga*). Head rounded, with widely separated small tubercles, similar to fig. 16, but higher; front more than $\frac{2}{3}$ its height, decidedly higher than wide, also tuberculate. Labrum with a fairly deep notch; setae as in *Charocampa*. Body decidedly swollen at first segment of abdomen, but not enough to withdraw the head.

Head decidedly longer than head. With a subdorsal line, and the normal obliques. Spiracles red with white ends (agreeing with the *Macroglossa* group, *Clarina*, and some specimens of *Protoparce*). Otherwise like *Choerocampa*.

In *A. versicolor* the horn is nearly twice as long as the head, thick and strongly down-curved; in *myron* it is shorter, straight and conical, but apparently it is exceptionally variable in all three species.

Clarina. Horn only about as long as head; tubercles of head very small and inconspicuous; otherwise wholly like *Ampeloecca*,—with continuous subdorsal. *C. syriaca*, of Syria.

Deidamia. Horn rather longer than head. Supraanal an acute equilateral triangle. Spiracles pale with a black bar on each side. Front full as wide as high. Body but little swollen. Otherwise like *Ampleocæca*.

C. syriaca and *D. inscriptum* are marked almost exactly like *A. myron*, but with evanescent obliques.

Amphion. Head irregularly roughened, without raised isolated tubercles, squarish, as in related genera. Supraanal as long as wide and acute; spiracles dark. Horn shorter than height of head. Front full as high as wide, third ocellus much enlarged (as in *Clarina* and *Deidamia* also). Body but little swollen. Otherwise like the related genera (I, figs. 48 and 53.)

Sphecodina. Body not at all swollen on the first abdominal segments. Head large, very rough in the last stage, but without raised tubercles; in the next to last as in *Ampelæca*. Front higher than wide, $\frac{3}{4}$ height of head. Clypeus broader than in *Deilephila*, etc. Labrum like *Pergesa*. Horn replaced by a wart; in the last stage similar to that of *Pholus*, in the next to last high, and cylindrical; before that surmounted by a slender horn, which rises, not as in *Pholus* from its posterior side, but from the middle. Supraanal wide.

Proserpinus (Fig. 3). Horn normal but rather short (*gauræ*) or replaced in the last stage by an eyespot, which may be nearly flat (*proserpina*), or with an obliquely conical center (*flavofasciata*, *juanita*). Head and skin smooth. Spiracles single-colored, yellow in *flavofasciata* and *proserpina*, black in *gauræ*. Head squarish, higher than wide in *proserpina*, full as wide as high in *flavofasciata*. Adfrontals only about $\frac{1}{4}$ as wide as front is high, with their setae i below the top of the front. Front nearly half as high as head, broadly triangular. Ocelli normal.

Labrum with a moderate or rather shallow notch, with the setae i and ii only half as far apart as the setae i are from each other (thus agreeing with the preceding genera rather than with *Hemaris*). Supraanal an equilateral triangle; joints of antennae nearly equal in diameter. In the next to last stage *flavofasciata* at least, has a horn similar to that in adult *gauræ*.

Macroglossa. Head and body nearly smooth, but marked by slight raised white tubercles. Head very small and round, the body sharply tapering toward it. Horn normal, longer than height of head. Adfrontals $\frac{1}{2}$ height of front in width, and with seta i higher than the top of the front. Third, fourth and lower ocelli evenly spaced, and very close together, nearer to each other than to the posterior. Front $\frac{3}{4}$ height of head; distance between setae i and ii of labrum $\frac{2}{3}$ that between the two setae i. True legs single-colored; spiracles red with white spots at the two ends. The genus shows likenesses to *Hemaris* on the one hand especially to *H. croatica*, which is very similar; and to the *Darapsa* group on the other, rather than to *Proserpinus*.

Hemaris (*Haemorrhagia*). Head rough and tuberculate cervical shield, etc., also rough, and skin generally with more or less distinct raised tubercles. Horn moderate, or long and slender. Front $\frac{1}{2}$ height of head. Otherwise as in *Macroglossa* even as to the coloring of the spiracles. The species I have seen make a very good graded series, from *Macroglossa* to *H. thysbe*.

H. croatica. Cervical shield no rougher than head, without any distinct anterior ridge; lower ocellus close to the next one as in *M. stellatarum*. Legs without any black. Head regularly rounded, not distinctly higher than wide.

H. rubens. Head and cervical shield with fine granulations separated from each other by about twice the diameter of a granulation, except toward the anterior edge of the cervical shield, where they are nearly in contact, and in a single even row. Front, and head as a whole higher than *croatica*, agreeing with the following species. Feet with a little black on the front of the coxae only. Horn rather short.

H. diffinis (typical). Cervical shield with the granules no larger than in *H. rubens*, but with the surface of the shield raised into ridges, so as to appear much rougher, considerably rougher than the head. The granules on the anterior edge make a ridge, but they are not confluent and the ridge is not well defined. The true legs have the femora marked with deep black brown.

I. diffinis axillaris. Head conspicuously rough. Anterior border of cervical shield of crowded granulations, not all in a single row; the shield decidedly rougher than in the normal form; horn longer than head.

H. thysbe. Even rougher than the preceding, the cervical shield with the granulations almost in contact, and on the anterior edge more or less confluent. Horn long and the outer part slender. Femora jet-black and very conspicuous.

In the next to last stage, *H. diffinis*, at least can hardly be separated from *Macroglossa*. The horn is minute.

Erinnyis (Dilophonola). Seta ii of labrum fully as high as i, and the setae i, ii and iii almost evenly spaced; iii, iv and v about evenly spaced along the outer edge. Supraanal sometimes with the rudiments of a pair of tubercles. Notch of labrum hardly $\frac{1}{2}$ its height, in depth. Head squarish, and full as high as wide; metathorax sharply humped; the abdomen abruptly smaller, and cylindrical. Horn short. In *E. edwardsii* the horn is somewhat shorter than the head, in *E. ello*, only a third as long, and only twice as long as thick. The tubercles on the anal plate are distincter in *edwardsii*, and the supraanal is narrower.

Pseudosphinx (I, Figs. 47 and 50). Cylindrical with slender horn. Fourth ocellus as far from the lower as from the first; front wider than high and nearly half as high as head. Labrum very shallowly notched, with the setae i and ii nearly on a level, and almost evenly spaced; iv directly below iii and much nearer to it than to v. vi not far from margin. Two conical spines on anal plate.

The following species were examined. I am especially indebted to Prof. J. B. Smith; Dr. Geo. Dimmock, Mr. William Beutenmuller, and Dr. H. G. Dyar, for the privilege of examining specimens in their own collections and in those of the institutions they represent. Exotic species are in italics; those from the far west, or from Florida only, are also indicated.

SPHINGINÆ

Acherontia atropos

Ilseis convolvuli

cingulata

Cocytius antæus Fla.

Phlegethontius quinquemaculatus

carolina (sexta), I, Fig. 51.

Atreides plebeius

Dolba hylæus

- Sphinx ligustri* II, Fig. 1.
 drupiferarum
 chersis
 kalmiae
 gordius, I, Figs. 39-41
 luscitiosa
Lintneria eremitus, II, Fig. 8.
Hyloicus pinastri, II, Fig. 10.
Lapara bombycoides, II, Figs. 4-5.
 coniferarum
Chlaenogramma jasminearum
Daremma undulosa
 catalpæ, II, Fig. 11.
 hageni ? (W)
Ceratomia amyntor, I, Figs. 45 and 49.

SMERINTHINÆ

- Pachysphinx modesta*, II, Fig. 7
 occidentalis (W)
Smerinthus ocellatus
 jamaicensis
 cerisyi
Paonias excacatus
 myops, I, Figs. 42-44.
 astylus
Amorpha populi
Dilina tiliae
Cressonia juglandis, II, Figs. 12 and 13.

CHOEROCAMPINÆ

- Deilephila lineata*, II, Fig. 9.
 gallii, I, Figs. 46 and 52
 euphorbiae
 lathyri
 vespertilio
Charocampa (Pergesa) elpenor
 porcellus
Charocampa (Hippotion) celerio, II, Fig. 15.
Charocampa (Theretra) alecto
Choerocampa (Xylophanes) tersa

PHILAMPELINÆ

- Pholus achemon*
 pandorus
 vitis (fasciatus)
 labruscæ (Figure only) Fla.
Daphnis nerii
Clarina kotschyi syriaca
Ampelophaga (Ampeloeca) myron versicolor
Ampelophaga (Darapsa) choerilis
Deidamia inscriptum
Sphecodina abbottii
Amphion nessus I, Figs. 48 and 53; II, Fig. 14.
Proserpinus proserpina, II, Fig. 3
 flavofasciata
 juanita
 gauræ
Macroglossa stellatarum

SESSINÆ

- Hemaris croatica* II, Fig. 16
 rubens (W)
 diffinis and form *axillaris*
 thysbe
Erynnis alope edwardsii Fla.
 ello Fla.
Pseudosphinx tetrio Fla., I, Figs. 47 and 50.

FIELD KEY TO THE SPHINGID CATERpillARS.*
OF THE EASTERN UNITED STATES.

- A. Horn completely wanting, head half higher than wide and triangular.....
Lapara confederarum and *bombycoides*
- A. Eighth abdominal segment bears a little hard nodule (caterpillar brilliantly marked with black, white and red)..... *Pholus fasciatus* (vitis)
- A. Eighth abdominal segment with an eyespot, otherwise unarmed..... B
- A. Eighth abdominal segment with a horn, otherwise unarmed..... F
- A. Eighth abdominal segment with a horn, mesothorax sharply humped or tuberculate..... *Lintneria eremitus*
- A. Eighth abdominal segment with a long horn, and thorax with four much shorter ones..... *Ceratonia quadricornis*
- B. Slanting white patches on the sides..... C
- B. Pale on the sides, obliquely mottled, eyespot white. *Pholus labruscae* (Fla.)
- B. Otherwise marked; eyespot dark-ringed..... D
- C. White patches are full three times as long as broad..... *Pholus achemon*
- C. White patches are $2\frac{1}{2}$ times as long as broad..... *Pholus pandorus*
- D. Checkered contrastingly with red and green..... *Proserpinus juanita*
- D. No red..... E
- E. Eyespot ringed with jet-black..... *Proserpinus flavofasciata*
- E. Eyespot ringed with brown..... *Sphocodina abbotii*
- F. Slanting lines on the sides, sloping upward toward the rear..... G
- F. Slanting lines, if present, running in the opposite direction..... Y
- G. Slanting lines dark and more than seven, with a double set on the dorsum..... *Amphion nessus*
- G. A single slanting line running up to the horn..... *Cocytius antæus*
- G. Numerous slanting lines, on the dorsum only..... *Cocytius cluentius*
- G. Slanting lines indefinite in number or evanescent; spiracle marked with two vertical bars, caterpillar a little humped..... *Deidamia inscriptum*
- G. Slanting lines six or seven, and distant..... H
- H. Head rounded, with two pair of vertical dark stripes; on Convolvulaceae..... *Herse cingulata*
- H. Head mostly with one or no vertical dark stripes; on other plants..... I
- I. Horn rudimentary..... *Pachysphinx modesta*
- I. Horn as long as head, or longer..... J
- J. Skin rough and granular, head triangular..... K
- J. Skin nearly smooth, but with the stripes marked with raised granulations..... O
- J. Skin smooth..... P
- K. Horn well defined and much longer than height of head..... *Cressonia juglandis*
- K. Horn about as long as height of head, and not very distinct from body, straight..... L
- L. The oblique stripes irregularly shaded with red patches..... *Paonias astylus*
- L. One of two pairs of red spots alone, or with one or two much larger than the others..... *Paonias myops*
- M. With a number of equal red spots or with none..... M
- M. With none, horn normally blunt, or blueberry..... *P. astylus*
- M. Horn always acute..... N
- N. Horn pink, violet or blue..... *Smerinthus cerisyi* and *jamaicensis*
- N. Horn normally blue-green..... *Paonias excrucatus*
- N. Horn normally yellow-green, yellow on the sides..... *Paonias myops*
- O. Head broad and rounded, granulated..... *Atreides plebeius*
- O. Head high and tapering, nearly smooth..... *Chlenogramma jasminearum*
- O. Head broad and tapering, nearly smooth..... *Phlegothontius rusticus*, and occasional specimens of *Sphinx chersis*, etc.
- P. First segment of abdomen much swollen, subdorsal stripe well developed..... Q
- P. Caterpillar nearly cylindrical, subdorsal stripe present on thorax only..... S
- Q. Subdorsal stripe complete..... *Ampelophaga myron*

* See "Field Tables of Lepidoptera (1906) p. 69.

- Q. Subdorsal stripe broken in the middle..... R
 R. Horn near twice as long as head, and down-curved..... **A. versicolor**
 R. Horn little longer than head and nearly straight..... **A. cheilanthi**
 S. With pale substigmatal bands on the segments which have obliques, making the obliques to form chevrons..... **Phlegethontius 5-maculatus**
 S. No stigmatal band..... T
 T. With the obliques showing no trace of red and edged above with a row of black spots, horn reddish..... **Phlegethontius californicus**
 T. Obliques not edged above with a row of black dots; usually with red or orange dots..... U
 U. Horn little longer than the height of the head, which is decidedly higher than wide..... **Daremma uncalosa**
 U. Horn about half longer than the head, which is as wide as high..... V
 V. Ground color very pale green (or the alternative pink or fawn)..... **Sphinx chersis**
 V. Ground color bright grass green (or crimson or brown)..... W
 W. Only six stripes are fully developed (pink); head broad and rough to the naked eye..... **Dolba hylæus**
 W. With seven equally well-developed stripes..... X
 X. Horn green, black at the sides, straight; stripes with pink..... **Sphinx gordius** and **luscitosa**
 X. Horn deep red (as also the stripes on the head); stripes violet..... **Sphinx drupiferarum**
 X. Stripes heavily marked with black, and often shaded with blue..... **Sphinx kalmiae**
 Y. With oblique stripes running up toward the front..... Z
 Y. With pale, transverse stripes; black..... **Pseudosphinx tetrio** (Fla.)
 Y. Catocala-like with small horn and a tubercle on middle of abdomen..... **Madoryx** (*M. pseudothyreus* occurs in Fla.)
 Y. With subdorsal eyespots..... A
 Y. Checkered or with patches of yellow dots..... C
 Y. Metathorax sharply humped with a dorsal eyespot..... E
 Y. More or less striped longitudinally..... F
 Z. Oblique stripes and subdorsal red..... **Proserpinus gauræ**
 Z. Oblique stripes and subdorsal yellow..... **Pachyllia ficus** (Fla.)
 A. A single eyespot on segment A1..... **Xylophanes porcus** ? (Fla.)
 A. All the eyespots alike..... B
 H. Ground color bright green; last eyespot quite like the others, lower part of head light..... **Deilephila lineata**
 B. Ground color olive green; last eyespot often stretching out toward the horn; head with a black band below..... **Deilephila gallii**
 C. Horn very slender..... **Daremma catalpa**
 C. Horn normal..... D
 D. Subdorsal yellow powdering if present continuous with that lower on the sides; lower part of face black..... **Deilephila gallii**
 D. Patches of subdorsal yellow powdering on each segment; or checkered with black and green; lower part of face concolorous..... **Deilephila lineata**
 E. Eyespot black with a pale ring..... **Erynnis alope**
 E. Eyespot black, with some red behind..... **Erynnis ello**
 E. Eyespot red, with a black center..... **Erynnis cramentum**
 F. Horn slender; with red dorsal stripe and two white stripes or rows of white spots on the sides..... **Hyloicus cupressi**
 F. Horn various; otherwise marked, not feeding on pine..... G
 G. Front edge of cervical shield raised and rough..... H
 G. Cervical shield lightly and evenly granulated.....
 Younger stages of **Proserpinus flavofasciata**, **Hemaris**, and very young stages of many **Sphingidæ**.
 H. Dorsal dark stripe edged on both sides with pale; horn much longer than head..... **Hemaris thysbe**
 H. Dorsal dark stripe vague; horn about as long as head..... **Hemaris diffinis**

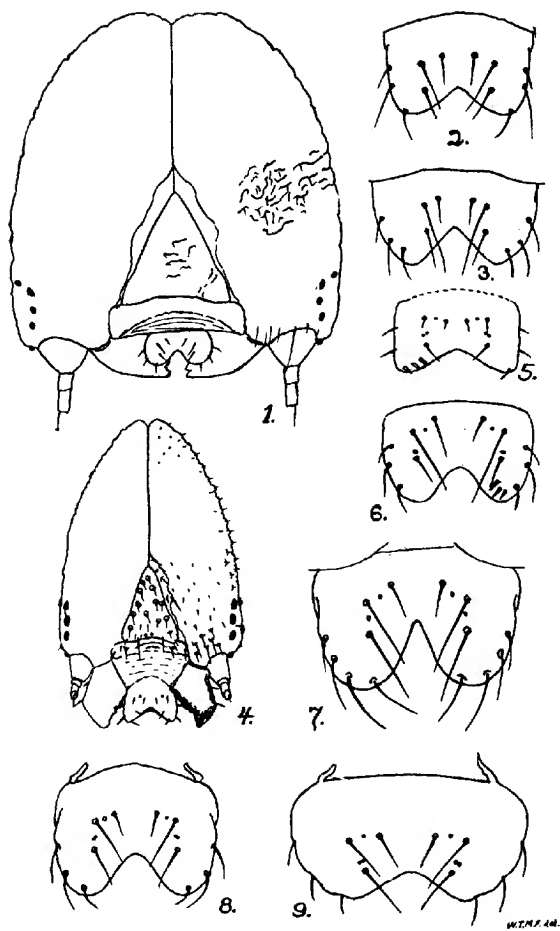
EXPLANATION OF THE FIGURES.

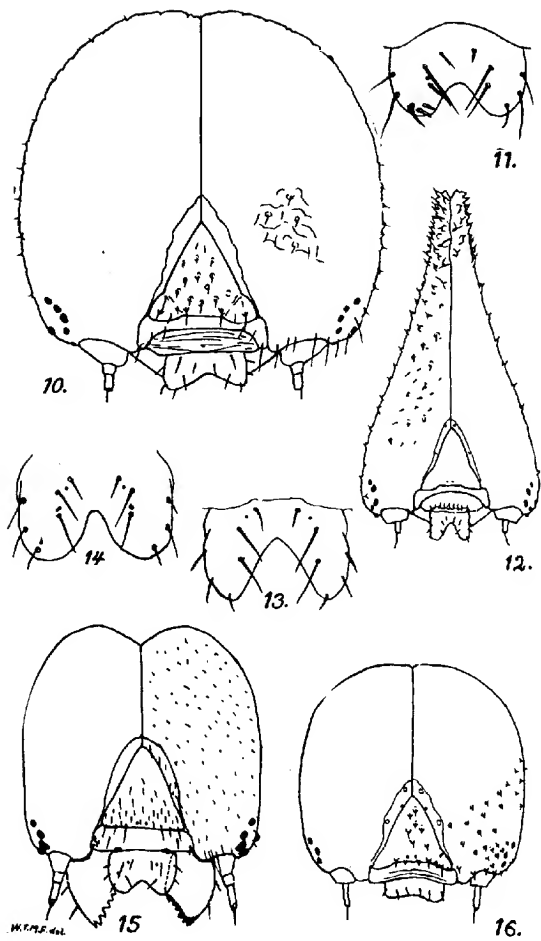
PLATE XVII.

- FIG. 1. Front view of head of *Sphinx ligustri*. It is fairly typical of the species in which the head tapers moderately, but more rounded out on the sides than the average. The front is also wider and less lobed at the bottom.
- FIG. 2. Labrum of *Hemaris thysbe*. Compare Annals E. S. A. III; Pl. xiv.
- FIG. 3. *Proserpinus proserpina*. Typical of the Semanophoræ; compare also Figs. 6 and 14.
- FIG. 4. Front view of head of last stage of *Ellema harrisii*. The triangular head, which is more typical of the Smerinthinæ.
- FIG. 5. Labrum of the same. *Hyloicus* is similar.
- FIG. 6. Labrum of *Hippotion celerio*.
- FIG. 7. Labrum of *Pachysphinx modesta*. *P. occidentalis* is the same, and the normal Smerinthinæ differ only in having one less marginal seta.
- FIG. 8. Labrum of *Sphinx* (*Lintneria*) *eremitus*, typical of the lower species of *Sphinx*. For one of the higher type see Annals E. S. A. III, Pl. xiii, Fig. 40, which is *S. gordius*, labelled "Dolba hylæus" in error. The species labelled *gordius* is certainly *S. drupiferarum*.
- FIG. 9. *Deilephila lineata*. The other species are about the same.

PLATE XVIII.

- FIG. 10. Front view of head of *Hyloicus pinastri*. *Sphinx drupiferarum* is similar in outline, and so are all the species described as having a broadly rounded head.
- FIG. 11. Labrum of *Datamina catalpæ*, showing seta iii high, as in the Semanophoræ.
- FIG. 12. "Next to last stage of *Cressonia juglandis*. In the same stage *Lapara* has the same peculiar shape.
- FIG. 13. Labrum of *Cressonia juglandis*, last stage.
- FIG. 14. Labrum of *Amphion nesus*. Typical.
- FIG. 15. Head of *Hippotion celerio*, showing the slightly squarish form which is most frequent in the Semanophoræ.
- FIG. 16. Head of *Hemaris croatica*. It is broader than our species of *Hemaris*, and resembles *Macroglossa* except in the small front.





SOME NOTES ON HEREDITY IN THE COCCINELLID GENUS ADALIA MULSANT.*

By MIRIAM A. PALMER.

It is the purpose of this paper to give a report of some experimental investigations in heredity which were made with four different forms belonging to the genus *Adalia* Mulsant. These forms shall herein be designated as *melanopleura* Leconte, *annectans* Crotch, *coloradensis* Casey, and *humeralis* Say.†

Melanopleura (Fig. A, Pl. XIX), as met with in this paper, is described as follows: Head black, with fine apical line of white, and with a whitish triangle next each eye with the apex pointing mesad and nearly reaching the median line. Sometimes a median strip of whitish connects these spots and extending forward to the apical line, which may also widen, leaves only a pair of black spots or brownish dots, one on either side of the median line on the anterior part of the head. (See head markings in Figures A, B, C, and F, Pl. XIX). Pronotum pale, with black M-shaped design and a lateral black spot, except in an unusually albinic form where the spot is absent or represented by a mere dusky area. The black spot when present may vary from a moderate sized area well enclosed by the surrounding white, to a large area which may break more or less widely through the surrounding white so as to connect with the M design. See pronotum markings in Figures A, B, and C, Pl. XIX). The basal marking is usually large in this form but may be rather small in some cases. Elytra brownish red and immaculate, or with faint dot on lateral margin of each elytron. Legs yellowish brown, darker on outer margin. Length 4-6 mm., width 3-4 mm.

Annectans, Figures B, C, and F, Plate XIX, includes quite a range of variation. The group as met with in this study is described as follows: Head as in *melanopleura*, pronotum as

* This paper is an outgrowth of breeding cage work with the *Coccinellids*, assigned me by Professor Gillette as a part of his Adams Fund project on Life Histories of the Plant Lice and Their Enemies.

† These determinations are according to Major Thos. L. Casey, who very kindly criticized my determinations of the forms referred to in this paper, excepting that *annectans* includes also an unusual and rather rare form (Fig. F, Pl. XIX), the status of which seems to me a little uncertain, but which Mr. C. W. Leng determines as *annectans*. Lacking any biological proof to the contrary I have included it under *annectans*.

given for *melanopleura* except that the basal marking is on the average somewhat smaller and is, in rare cases, even absent. The lateral black spot also is absent in an unusually albinic form, Figure F, Plate XIX. Elytra reddish yellow, usually lighter than *melanopleura*, quite yellowish for several weeks after emergence, becoming redder with age, though some never develop much of the red color. In the individuals reared of the more albinic form, Figure F, Plate XIX, the red color began to appear immediately after emergence but was paler in the region of the spots, giving a sort of blotchy appearance. This paler area may persist even in old beetles which have hibernated. Each elytron typically with a longitudinal posteriorly pointed black dash from the base at each side of the suture, and two sub-basal spots, the outer more basal, also with a transverse series of three black spots just before the middle, and two more at apical fourth, the outer very close to the margin. These black spots may vary from mere dots with some absent, to large blotches which may have more or less tendency to confluence; so that in color pattern many resembled *ovipennis* Casey, and a very few came very close to *transversalis* Casey as figured by Johnson.* Mr. Casey, however, to whom I submitted specimens of these beetles, says that they are not his species as they do not show the proper punctuation. Some specimens show a rather definite pattern of red spots, two on each elytron, one a large oblong spot at the humerus and the other a smaller round spot close to the suture and between the middle and apical series of black spots. Legs and size as in *melanopleura*.

In the more albinic form, Figure F, Plate XIX, the anterior spots were always lacking and the middle and apical series were irregularly represented. Altogether this form differs from the rest of the group in three respects; namely, in lacking the anterior or basal elytral black spots, the absence of the lateral black spots on the pronotum, and in the presence of the redder coloration of the elytra. Three individuals of this form appeared in one batch of *annectans*, and one in another batch of *annectans*, also two from a batch of larvae, from *melanopleura* parents, which produced both *melanopleura* and *annectans*. In these broods there were also some individuals which might be

* Johnson, Roswell H., 1910—Determinate Evolution in the Color Pattern of the Lady-beetles, Carnegie Institution of Washington. Pub. No. 122.
Papers of the Station for Experimental Evolution, No. 15.

considered as intergrading forms to some extent. This form presents a rather strikingly different appearance from the rest of the group, since all of these characters seem as a rule to go together, making a rather pronounced gap in the series of variation. It seems indeed to be closer to *coloradensis* than to *annectans*. Furthermore, among the 109 *annectans* which were reared from eggs of two *annectans* females and two *melanopleura-annectans* hybrid females, mated with one *annectans* male and one *melanopleura* male, not one of these forms appeared, which fact seems to show that it is not a common fluctuating variation at least. It seems that the heredity might be segregate and experiments are now in progress to determine this point. It is on this account that I have thought best to call attention to it separately though for the rest of this paper it will be included under *annectans*.

Coloradensis Casey, Fig. E, Pl. XIX, is described as follows: Head black with fine apical margin of whitish, and triangular pale spot next each eye as found in *annectans*. Pronotum black with very fine apical pale margin sometimes obliterated, the posteriorly pointed median pale dash from the apical margin very small when present, sides with same pale pattern as *melanopleura* but lacking the black lateral spot, basal marking absent. Elytra brownish red, about the same color as *melanopleura*, with a duplex black spot at the middle, sometimes in the form of a band, sometimes appearing as two separate spots, also a similar series of spots, two in number at apical fourth, the inner one the larger. Legs and size as in *melanopleura*, but the shape perhaps a little more narrowly oval.

Humeralis, Say, Figure D, Plate XIX; Head same as in *melanopleura*, except that sometimes a different pattern appears as shown in Figure D, Plate XIX. Pronotum black with fine apical line and narrow side margins pale, apical line sometimes obliterated, basal marking always absent. Elytra black with a large oblong yellowish red to bright red spot at humerus and another small round one at three-fifths and close to the suture. The red marking on the elytra seems identical with the red pattern above mentioned as appearing in some specimens of *annectans*. Legs and size same as given for *melanopleura*, shape usually a little more rounded posteriorly.

The work with these forms was at first undertaken merely for the purpose of obtaining specimens for life history drawings of *melanopleura* and *annectans*. In rearing these forms the

fact of their interbreeding with each other and with *humeralis* was discovered, and then the work was directed along the line of heredity investigation. About four hundred beetles were reared to maturity from about three thousand eggs hatched. These beetles proved much more difficult to rear than the larger species such as *Hippodamia convergens* and *Coccinella quinque-notata* because of their more limited range of food and more delicate constitutions. All large aphids brought disaster in the breeding cage and sometimes even the small cottonwood louse, *Chaitophorus populicola* Thos. was rejected. In the latter case it was perhaps due to an odor left by a certain species of attendant ants, since these lice did not always prove objectionable. One feed of unfavorable lice would sometimes cause the death of from one-half to nine-tenths of a cage of larvae.

Work was begun with these beetles with the capture, May 13, 1910, in the foothills near Fort Collins, Colorado, of a pair of *annectans*. Eggs of this female were laid in the laboratory and the larvae reared. When the beetles eight in number emerged, four proved to be like the parents and four were *humeralis*. Three subsequent batches of larvae giving nine adults, were reared from eggs laid by this female and her spotted daughters with the result that three of the beetles were *annectans* and six were *humeralis*.

For the purpose of obtaining more material and also of ascertaining how frequently such mixing occurred, two or three dozen pupae of this species were collected outdoors, and as soon as the beetles emerged and the colors developed the different forms were isolated in separate cages. About fifteen percent were *humeralis* and the rest were about evenly divided between *melanopleura* and *annectans*. The *humeralis* beetles escaped by accident, but from the eggs of the other forms a considerable number of larvae were reared to maturity. From the eggs laid in the *melanopleura* cage thirty beetles were reared, and in each batch a large proportion were *annectans*, sometimes over half the batch and once the entire batch. Practically the same proportions were obtained from eggs of one or two females captured at other times. Besides the forms already mentioned three individuals of *coloradensis* appeared among the progeny of the above mentioned cage. Unfortunately these were not used for breeding purposes but were pinned up and put in the collection. Breeding experiments are now, however, in progress with this form.

From the cage of *annectans* only *annectans* were obtained. Twenty-five adults were reared from eggs laid in this cage, and fifty-seven from eggs laid by a female tested in a way to be explained later, making eighty-two beetles in all, and every one proved to be *annectans*. The eggs of one *annectans* female captured out of doors produced several *melanopleura* but this female had probably been fertilized by a hybrid male or even by both *melanopleura* and *annectans* males before it was captured.

The *humeralis* beetles reared from the first pair mentioned were used for breeding purposes and all the individuals reared came true to type, about thirty beetles maturing.

It was now indirectly evident that mixing was quite common between *melanopleura* and *annectans* and that it sometimes occurred between *annectans* and *humeralis*, but there was no evidence that it occurred between *melanopleura* and *humeralis*. To ascertain whether this latter were possible and also to make the actual crosses in the other cases in order to further investigate the law of heredity, efforts were made to cross *humeralis* as often as possible with *annectans* and *melanopleura*. *Humeralis* was found to hybridize just as freely with one form as with the other. No more difficulty was encountered than would be expected even among members of the same form under the same circumstances. On one occasion an *annectans* male chose a *humeralis* female even though a female of its own kind was present in the cage.

Unfortunately only one female of *humeralis* was available for this purpose sufficiently early in the season, but there were several males which proved capable and these were crossed with females of both *melanopleura* and *annectans*. The female of *humeralis* that was used was probably the one that produced all of the above mentioned 30 *humeralis*, all true to type, she, at any rate produced a large proportion of them. This beetle was crossed with an *annectans* male but she died so soon that only two beetles were reared from this union. They were *annectans* but were too feeble for further breeding. An *annectans-humeralis* hybrid female was mated with a *melanopleura* male and later with an *annectans* male. This female had previously been kept in a cage with its brothers and the eggs laid had produced seven *humeralis* and four *annectans*, but after these crossings no more *humeralis* appeared though forty-seven beetles were reared. Three crosses were made by means of the *humeralis* males and *melanopleura* and *annectans*

females and from these 169 beetles were reared in the first generation. All but one were either *melanopleura* or *annectans* according to the composition of the female. This one exception was a *humeralis* beetle. A noticeable character of the progeny of these crosses was the greater vigor of the individuals so that a larger percent matured as compared with the purer strains. From one of the above three pairs, an *annectans* female and a *humeralis* male, the first generation of which consisted of fifty-seven *annectans*, four second generation beetles were reared and they proved to be two *annectans* and two *humeralis*. The beetles then refused to lay any more eggs and seemed to be preparing for hibernation. They had been unavoidably subjected for a few days to a temperature low enough to stiffen them up considerably and cause them to nearly cease eating and the subsequent removal of them to an almost summer temperature, though it caused the eggs to hatch in half the time they had under the low temperature and increased the appetites and rate of growth of the larvae quite remarkably, failed to cause the beetles to lay any more eggs. Work had, therefore, to close for the season at this interesting point, and the beetles were put into hibernation.*

From these crosses there is another lesson to be learned besides the relation of *annectans* and *melanopleura* to *humeralis*, namely; something about the heredity between *melanopleura* and *annectans* themselves. The process of mating these forms with *humeralis* which is recessive to both, served as a test of the germinal composition of the member of the pair carrying the dominant characters. In the case where two *melanopleura* females, which had been isolated from *annectans* from time of emerging were crossed with *humeralis* males there were produced 29 *melanopleura* to 25 *annectans*, and 31 *melanopleura* to 26 *annectans* respectively. *Melanopleura* was in each case a little in excess of 50 percent. In the case of the *annectans-humeralis* hybrid female mated with the *melanopleura-annectans* male the progeny was 19 *melanopleura* and 28 *annectans*. The higher percent of *annectans* was doubtless due to the fact that an *annectans* male was put into the cage during the latter

* Just as this article was ready to send to the publisher a lot of second generation beetles, from the *melanopleura* females crossed with the *humeralis* males, emerged. From the eggs of the first generation *melanopleura-humeralis* hybrids there were reared 19 *melanopleura* and 7 *humeralis*. From the eggs of the first generation *annectans-humeralis* hybrids there matured 12 *annectans* and 5 *humeralis*. These figures come very near to the Mendelian ratio for progeny of hybrids.

part of the period, because just before the last three batches the proportion was 16 *melanopleura* and 18 *annectans*, and the last three batches gave 3 *melanopleura* and 10 *annectans*, thus making a sudden change in the proportion. This male was in all probability pure *annectans* as there has not been found, in my experience, any proven case of *annectans* carrying *melanopleura* characters. The characters carried by the female could have had no influence whatever in the results, since neither of the characters carried by the female was dominant to the characters carried by the male. Either the *melanopleura* or the *annectans* characters of the male would realize themselves whether they met an *annectans* or a *humeralis* character of the female. These results approximately show that the *melanopleura*-*annectans* hybrids carry the characters in the proportion of half and half. The somewhat high percentage of *melanopleura* obtained in these cases was more than balanced by the extremely low percentage obtained in the case of the progeny of the cage of *melanopleura*-*annectans* hybrids, in which case *melanopleura* constituted less than half of the progeny when it should have constituted three-fourths. The mortality in this latter case, however, was so great that the data are hardly sufficient.

Another *melanopleura* female from *melanopleura*-*annectans* hybrid parents after being fertilized by some of its *melanopleura* brothers was isolated for a few days, during which time it laid three batches of eggs. From these eggs were reared 10 *melanopleura*, 3 *humeralis*, and 1 *annectans*. Excepting the one *annectans*, this was just the right proportion for the progeny of two hybrids according to the Mendelian law. This *annectans* individual, (if it did not get in by mistake which was very unlikely, great care having been exercised) must have been due to fertilization by a *melanopleura*-*annectans* male probably before the *melanopleura*-*humeralis* male. The female was then mated with a *humeralis* male and after that 14 adults were obtained, 6 *melanopleura* and 8 *annectans*. The results in this case seem to indicate that there had been a cross between the *melanopleura* ancestors of this female and *humeralis*, while still in nature and that in the first generation reared in captivity the dominant *melanopleura* had kept it concealed, so that it was not until the second generation that the crossing between two hybrids happened to take place, thus allowing the *humeralis* character to appear.

From the cross between an *annectans* female (reared from *melanopleura* parents) and a *humeralis* male 57 beetles measured all *annectans*. This showed the female to be pure strain though descended from *melanopleura* parents.

The foregoing results are given below in tabulated form:

	mel.	col.	ann.	hum.	total
<i>Crosses</i>					
1 Male— <i>annectans</i>			2		2
Female— <i>humeralis</i>			57		57
2 Male— <i>humeralis</i>			2	2	4
Female— <i>annectans</i>			25		54
3 Male— <i>humeralis</i>			19	7	26
Female— <i>melanopleura</i> *.....			12	5	17
4 Male— <i>humeralis</i>			31	1	58
Female— <i>melanopleura</i> *.....			26		
5 Male— <i>melanopleura</i> *.....			16	18	
and later <i>annectans</i>			3	10	47
Female— <i>annectans-humeralis</i> hybrid.....					
<i>Humeralis Hybrid</i>					
Female— <i>annectans-humeralis</i>			7	10	17
Male— <i>annectans-humeralis</i>					
Female— <i>melanopleura-humeralis</i>	9		1	3	13
Male— <i>melanopleura-humeralis</i> (probably).....					
Also <i>melanopleura-annectans</i> (prob.).....					
Female— <i>melanopleura-humeralis</i>	6			8	14
Male— <i>humeralis</i>					
<i>Melanopleura-annectans Hybrids</i>					
Cage of males and females—offspring.....	11	3	16		30
Female captured, male <i>annectans</i> ?.....	7		6		13
Two females and one male mated with recessive.....	76		69	1	
(See crosses 3, 4 and 5)					
	94	3	91	1	
<i>Annectans</i>					
Cage of males and females—offspring.....			19		19
One female, captured, male unknown, offspring.....			6		6
One female with <i>humeralis</i> male (See cross 2)—offspring.....			57		
			82		
<i>Humeralis</i>					
One female with 3 males—offspring.....				30	30
(Female used later in cross 1)					
Total.....					407

* *melanopleura-annectans* hybrid.

From the foregoing results the following conclusions seem to be quite evident:

- I. *Melanopleura* is dominant over *annectans*, *coloradensis*, and *humeralis*, and the heredity is segregate.
 - a. Over *annectans* since
 - a. The hybrid form between *melanopleura* and *annectans* is *melanopleura*. Of the progeny, 30 in number, of a cage of *melanopleura*, *annectans* constituted over half. In the progeny of two females and one male tested by mating with *humeralis* there appeared 76 *annectans* and 69 *melanopleura*, altogether, which is very close to the Mendelian ratio for the segregation of characters in hybrids.
 - b. *Annectans* has in no case given evidence of carrying *melanopleura* characters. The 25 progeny from a cage of *annectans* showed no *melanopleura* characters nor did any of the 57 progeny of the *annectans* female mated with *humeralis*.
 - b. Over *coloradensis* since the hybrid form between *melanopleura* and *coloradensis* is *melanopleura* as is shown by the fact that 3 *coloradensis* appeared among the offspring of *melanopleura* parents.
 - c. Over *humeralis* since
 - a. The hybrid form between *melanopleura* and *humeralis* is *melanopleura*. In the first generation from three crosses of *melanopleura* with *humeralis* or with *annectans-humeralis* hybrids, *humeralis* appeared but once among 159 individuals. A *melanopleura-humeralis* female mated with its brothers gave 9 *melanopleura*, 1 *annectans*, and 3 *humeralis*. The same female mated with a *humeralis* male gave 6 *melanopleura* and 8 *humeralis*, approximately showing the segregation of characters to be according to the Mendelian law. The second generation from crossings of *melanopleura* with *humeralis* consisted of 19 *melanopleura* and 7 *humeralis*.
 - b. *Humeralis* has given no evidence of carrying *melanopleura* characters. The 30 offspring from *humeralis* parents all came true to type.
- II. *Annectans* is dominant over *humeralis* since
 - a. The hybrid form between *annectans* and *humeralis* is *annectans*. In the cross between *annectans* and *humeralis* *humeralis* did not appear at all in the first generation of 57 progeny, but did appear in half of the second generation which consisted of 4 beetles. *Annectans-humeralis* hybrids mated with each other produced 7 *annectans* and 10 *humeralis* in one case, and in another 12 *annectans* and 5 *humeralis*.
 - b. *Humeralis* has given no evidence of carrying *annectans* characters, as shown by the 30 offspring of *humeralis* parents all true to type.

This subject is still unfinished and experiments are now in progress to determine the relation of *coloradensis* and the rather albinic form of *annectans* to the other forms.

It would be interesting to interbreed these forms with other species of *Adalia*, especially with the European *frigida* Schneider and with *bipunctata* Linneaus.

Observations were also made on the beetles used in the foregoing experiments for the purpose of ascertaining the heritability of the characters of the spots on the elytra in *annectans* and of the markings of the pronotum in this same form and in *melanopleura*. The progeny resulting from the mating of *annectans* and *melanopleura* beetles with the recessive *humeralis* were examined when the number was large enough to afford sufficient data. The beetles in these cases were particularly advantageous for this purpose because the dominant characters would be the only ones to show in the first generation, thus reducing the number of strains which would appear to one or two. In the case of the *melanopleura-annectans* hybrids there would be one strain of *annectans* and one of *melanopleura*, which would afford a very simple series and show very plainly whether these characters behave at all as unit characters or whether they seem to be fluctuating variations. The results are shown in the drawings Figures 2 to 7, Plates XX to XXII.

In the markings of the pronotum, special attention was paid to the character of the lateral black spot and the extent to which was it enclosed by the surrounding white. The median posteriorly pointed dash of white from the apical margin and also the basal marking of whitish are sometimes very small or even absent; but in this study only secondary attention was paid to these and the drawings, except curve (e), Fig. 7, Plate XXII, are arranged in series according to the aforesaid black spot. The pronota of *melanopleura* and *annectans* are arranged separately in each case.

In the case of the elytra primary attention was paid to the confluence of the spots, and the series is arranged according to the number of confluences in each case. The parents of each series are drawn in full or designated above and the first generation progeny in a row below. The numerals below each drawing indicate the number of individuals in that class. As the *humeralis* parent seems to have no influence on the char-

across of the first generation it was not thought necessary to draw this parent.

Figure 2, Plate XX represents the *annectans-humeralis* hybrid female and her progeny resulting from union with a *melanopleura-annectans* hybrid male, and also for the last few days of the experiment, with a pure *annectans* male. The numbering of the spots is after Weise taken from Johnson 1910. In this case the progeny would contain four strains of *annectans*, one from the mother, one from the *melanopleura-annectans* father, and two strains from the *annectans* father, which, however, could hardly have affected more than the last three batches of eggs. This would be just the number of strains to be represented if two members of *annectans* were mated. The males in this case were both lost and so can not be shown in the figure. Of the batches after the *annectans* male was introduced, in the elytra series, one beetle was in class (d), six in class (e), three in class (f), and one in class (i). In the pronota series four were in class (k) and seven in class (l). There was considerably less variation among these than in the foregoing batches, but whether it was due to the *annectans* male or to environmental influences can not be ascertained with certainty; but as these were reared later in the season than the foregoing batches, during the latter part of August and the early part of September, during which time an unusually cold wave occurred, the only environmental influence would probably have been a lower temperature. This factor, however, would, from the experience of Tower* and Johnson, be expected to produce a melanic effect, but here the difference was albinic rather than melanic, so the case does not seem to be explained by the environmental factor, and unless it was produced by some unknown cause, seems most probably to have been due to heredity factors introduced by the *annectans* male.

It will be noted in this case, Figure 6, curve (a), Plate XXI, and Figure 7, curves (a), and (b) Plate XXII, that all of the beetles, of both *melanopleura* and *annectans*, which were reared from this female were rather at the albinic end of the scale as to both elytral and pronotal characters. In the elytra none have more than two full confluences and the mother ranks at

* Tower, William Lawrence, 1906. An Investigation of Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*. Carnegie Institution of Washington, Pub. No. 48.

about the middle of the series and at one of the highest points of the curve. In the case of the pronotum the mother was decidedly more melanic than the apex of the curve for either *annectans* or *melanopleura*. The curves for these two forms were not alike, *annectans* having the greatest number, 40 per cent at the albinic end of the scale with the black spot well enclosed by the surrounding white. In the *melanopleura* series only 11 per cent were at this point, the largest number, 83 per cent, having the black spot rather weakly enclosed. None of the *annectans* here showed the red pattern on the elytra, as shown in Figure B, Plate XIX, though the mother shows it faintly.

Figure 3, Plate XX, represents the *annectans* female crossed with *humeralis* male. In this case we would expect to find only two strains of *annectans*. Here, however, the variation was considerably broader than in the former case where four strains were represented, the curve beginning at the same point of albinism as the former case and extending to four and a half confluences (that is to four and a pronounced tendency to a fifth confluence), Figure 6, curve (b). The mother was several degrees more albinic than the highest point of the curve. Note here that in the mother there is an absence of spot 4 and also that there is a small spot between spots 1 and 2, which, though very unusual, probably denotes tendency to confluence between spots 1 and 2. Neither the presence of this extra spot nor the absence of spot 4 show in any of the progeny examined, though both confluence and tendency to confluence appear between spots 1 and 2. The mother of these seems to have shown nothing of the red pattern mentioned above and shown in Figure B, Plate XIX, but in the 37 offspring, 9 showed it very plainly, 16 moderately plain, 4 faintly, and in 6 it was absent.

Figure 4, Plate XXI shows a *melanopleura-annectans* hybrid female, crossed with a *humeralis* male, and her first generation progeny. Here there can be but one strain of *annectans* to appear in the progeny. The curve of variation, Figure 6, curve (c), Plate XXI, covers a somewhat wider range of variation than in the case of the first instance, curve (a) where four strains are represented, the largest number of confluences being three. Here 23 out of 27 or 85 percent lack spot 6. In the pronota of *annectans* a peculiarity was observed in that sometimes either the basal marking or the apical median dash were lacking.

For these pronota two curves were given, Figure 7, curves (d) and (e), curve (d) to show the variation of the lateral spot only and curve (e) to represent the general melanism when the other markings are considered, each degree representing about the equivalent of the melanism of the state of the lateral spot as given in the legend for the respective columns. The curve for *annectans* in this series was much broader than that for *melanopleura*. The mother was rather toward the albinic end of the series for *annectans* and at the melanic end for *melanopleura*. All of the *annectans*, 27 in number, had the red spots on the elytra, as shown in Fig. B, Plate XIX.

Figure 5, Plate III, shows another *melanopleura-annectans* hybrid, female mated with a *humeralis* male, and her first generation progeny. Here again would be but one strain of *annectans*. The range of variation in the elytra of *annectans* was not very broad, showing none of the more albinic forms, the curve, Figure 6, curve (d), Plate XXI, beginning at one confluence and extending to three and a half confluent. In the pronota of the *annectans* series, Figure 7, curve (g), Plate XXII, uniformity almost obtains, 93 per cent having the lateral spot well enclosed and 7 per cent being one-fifth enclosed. In the *melanopleura* series, however, the curve, Figure 7, curve (h), Plate XXII, is very broad extending to a degree of melanism that is quite rare. The mother ranks at the albinic end of the scale though the highest part of the curve for her *melanopleura* offspring is four degrees further to the melanic end of the scale.

GENERAL OBSERVATIONS.

In comparing the curves for the elytra it must be born in mind that the chief points of comparison are the melanic positions of the range and highest points of the curves. Since the number of individuals represented by each of the curves was not uniform, the exact number on any one line shown by the different curves is not truly comparable; only the melanic position of high and low points and range in each curve can be compared with the same in another curve.

It will be noted that each curve has one or two points that are much higher than any other points in the curve, and that these high points in the different curves vary greatly in melanic position, also that the curves vary considerably in their range. It seems as though these high points in the curves might represent centers of variation. The curves would then signify that different strains of these beetles have different centers of

variation and different scopes of variation. Curve (c), Figure 5, Plate XXI, which represents but one strain of *annectans* covers a wider range than curve (a) which* represents four strains. Curve (d), which also represents one strain is quite narrow, seeming to signify that this strain had a greater degree of constancy than the others. The mother in each of these cases occurred within the range of variation for her progeny but not always at the highest point of the curve though in both of the instances where this observation was possible she occurred at one of the high points, see curves (a) and (b), Fig. 6, Plate XXI. Two of the mothers being *melanopleura* had no place in the elytra series, and since in the cases where the mother was *annectans* two or more strains were represented, the fact of the highest part of the curve not being at the same position as the mother might in this case be explained as due to one of the other strains involved.

There seemed in some cases to be a certain measure of heritability of different characters in the color pattern of the elytra. The absence of spot 6 in Figure 4, Plate XXI, seemed to be inherited to a large degree since it was lacking in 21 out of 27 beetles. The mother being *melanopleura* could not be observed on this point. This spot seems from my observations to be the one most frequently lacking in this form, indeed almost the only one except in a small minority of beetles. Spot 4 was absent in only three beetles in this study, in Figure 3 (a), Plate XX, and in two others not drawn but ranked with (f) and (g) respectively in Figure 2, Plate XX, spot 5 was faint in one, Figure 3 (c). The absence of spot 4 seemed not to be inherited in these cases, as no case of absence occurred in the 37 progeny of the mother, Figure 3 (a), which lacked it, and it appeared only twice in the 30 offspring in Figure 2, Plate XX.

Some observations were made on the order in which confluences take place. Spots 6 and 7 seemed to be the first as a rule to connect, as in this study there was only one instance where a beetle showed confluences and had these spots separate, see Figure 3 (e). There were three such cases where spot 6 was absent, but even in the case of absence there was often a projection toward its position from spot 7 as though in these instances the confluence was even more persistent than the spot itself. After this confluence no further order was observed except that between spots 4 and 5 it seemed to be the most unusual and perhaps the last in order.

In the case of the pattern of reddish spots on the elytra of *annectans* Figure B, Plate XIX, it seemed as though there might be segregation in some cases at least, and that the absence of the character was dominant to its presence. In the series in Figure C, Plate XX, it shows faintly in the mother (the dimness may be due to fading after death as this character was not recorded during life) and it was plainly evident in the mother and a brother of this beetle, in fact in all of the individuals of this strain that have been preserved. It shows in none of the 30 progeny of this beetle, but this absence may be explained as due to the males, which being lost, can not be examined as to their possession of the character.

In the series in Figure 3 where the mother does not show the marking but carries two strains of *annectans*, it appeared in five-sixths of the beetles to a greater or less degree. As the male in this case was *humeralis* both of these strains must have come from the mother and its absence in her development would seem to signify the dominance of the absence of the character over its presence. The proportion, however, found in the progeny seems rather puzzling unless the *humeralis* character from the male could have had any influence in the proportion, which seems unlikely.

In the series in Figure 4, Plate XXI, it appeared in all of the 27 *annectans* progeny. The mother, being *melanopleura* of course does not show it. In the series in Figure 5, Plate XXI, some show it and some do not. The exact number in each case can not be determined as some of the beetles have developed so much of the red color in their elytra during hibernation that it is impossible to tell with certainty whether they possess the character or not. The mother being *melanopleura* of course does not show the character. The fact that some clearly show its presence and others just as clearly show its absence when they are all from one strain of *annectans* seems to be evidence against segregation in this case.

In the pronota curves in Figure 7, Plate XXII, the matter is a little more complex as there are both *annectans* and *melanopleura* to be represented for each female except one, Figure 2, Plate XX. As the curves for these two forms even when from the same parents were different in every case not only in the position of the apex but also in range and sometimes very different, it would seem that each strain keeps distinct; that is, the pronotal characters of *annectans* do not mix with those of *melanopleura*.

When, however, the characters of the mother are compared with those of her offspring which are of the same form as herself, little uniformity was found. In no case did she rank at the highest point of the curve, neither did she ever occur at the lowest point, nor ever outside of the range of variation for the offspring. There seemed to be some degree of heredity but it was not constant. The results appear a good deal the same as in the elytra, that there are centers of variation and a certain limit of range that were inherited to a greater or less degree, but with no evidence of segregation of unit characters such as occurs between *melanopleura*, *annectans*, and *humeralis*.

ADDENDA.

Since sending the foregoing article to the publisher results have been obtained in the experiments concerning the relation of *coloradensis*, the so-called albinic form of *annectans*, and a similar form of *melanopleura* to the other forms treated. The albinic form of *annectans*, so-called for want of a better name is above described separately under *annectans* and figured at F, Plate I. The albinic form of *melanopleura* is identical with that of *annectans* in pronotal characters, namely, it lacks the lateral dot, the lateral margin of the pronotum being broadly pale as in *coloradensis*; in all other characters it agrees with *melanopleura*. The results obtained are tabulated as follows:

Parents				1st gen. Offspring						
Male		Female								total
Appearance	Characters carried†	Appearance	Characters carried†	M	al. M	al. A	A	C	H	
C	C and H	H	H					4	3	7
unknown	M and A	al. A	C and A	4	2	1	1	3	2	8
H	H									5
H	H	al. M	C and M	3				1		4
C	C and H	M	M and H	6	7			4	6	23
al. A.	C and A	M	M and H	3	3			3	2	11
al. A.	C and A	al. A.	C and A			13	5	5		23
		H	H				7		10	17
‡A	A and H									
		A	A and H				11		2	13
al. M.	C and M	al. M.	C and M	4						4
Total.				16	16	14	30	18	21	115

* A means *annectans*; C, *coloradensis*; H, *humeralis*; al. A, albinic *annectans*; al. M, albinic *melanopleura*.

† These are given as shown by the offspring when not known from pedigree breeding.

‡ This male was, judging from appearance, an intergrade between *annectans* and albinic *annectans*. It lacked the basal spots on the elytra but possessed the lateral dot on the pronotum, which latter seems to be the ultimate distinguishing character.

These results seem to furnish conclusive evidence

1. That *coloradensis* is a good variety or type equal with *melanopleura*, *annectans*, and *humeralis*, acting as a unit character in heredity.
2. That when crossed with *annectans*, *coloradensis* produces a blended hybrid, in both elytral and pronotal characters, namely the form above referred to as an albinic form of *annectans*.
3. That when crossed with *melanopleura* a blend is produced in the pronotal characters, identical with the *annectans* blend; but in the elytra *melanopleura* dominates entirely.* This form was mentioned in the description of *melanopleura* as a "more albinic form."
4. That when crossed with *humeralis* *coloradensis* dominates perfectly so that the hybrid form is indistinguishable from the pure strain of *coloradensis*.

It seems that in every instance the more albinic character dominated over the more melanic one; for example: immaculate elytra, in *melanopleura*, dominate over the spotted ones of each of the other forms. The absence of the black lateral dot in the pronotum, in *coloradensis*, dominates over its presence in each of the other forms. The presence of the whitish basal marking on the pronotum, of *annectans* and *melanopleura*, dominates over its absence in *coloradensis* and *humeralis*. The absence of the basal elytral spots, in *coloradensis*, dominates over its presence in *annectans*. The usual absence of confluence in the median and apical series of spots in *annectans* dominates over the confluence in these spots in *coloradensis*. *Humeralis* which presents the most melanic characters in every particular in both elytra and pronotum is perfectly recessive to each of the other forms.

The inheritance of the faint lateral dot on the elytra in *melanopleura* was observed in the specimens at hand but no law was ascertained. It seems to be a mere fluctuating variation.

The single *humeralis* beetle mentioned in the article as appearing among the first generation offspring in the 4th cross in the table, between *humeralis* and *melanopleura* parents, was tested in breeding. It proved to be a male and was put into a cage with two *humeralis* females, from the eggs of which seven progeny were reared to maturity. All of these were *humeralis*

* This statement is to be reconciled with the statement in the foregoing article that *melanopleura* is dominant over *coloradensis* by the fact that at that time the hybrid was considered as only a variant of *melanopleura*.

which seems to prove that the beetle in question was pure strain. This beetle may possibly have gotten into the cage by mistake in spite of the great care exercised as several dozen cages containing larvae of all the forms were being tended and cleaned daily.

Five other offspring were reared from *humeralis* beetles obtained in these experiments, and these all came true, making 42 progeny in all reared from *humeralis* parents, breeding true in every instance.

Two *humeralis* beetles without dorsal spots were obtained as the progeny resulting from a cross between a *melanopleura* male, (evidently a *humeralis* hybrid) from out of doors, with an *annectans-humeralis* female representing the third generation of *humeralis* reared in the laboratory. All of the ancestors and progeny, two in number, of this female, by a former mating showed the dorsal spots normally developed. These two beetles were the only progeny obtained from this union and efforts to rear offspring from them, though they proved to be male and female, have thus far been fruitless, seemingly due to a weak constitution as the eggs hatch poorly. The male seemed weak and both beetles died soon. It would seem from this case that the absence of these spots dominated over its presence, which is contrary to the behavior of heredity with regard to the other characters of this group. If this is not the case the strain in the laboratory must have carried this character of absence through three generations without it having a chance to meet its equal so as to be able to realize itself.

Another cross which was made between an *annectans* male and a *humeralis* female last August but which laid no eggs until this, the following spring, produced in the first generation 26 beetles, all *annectans*. The *humeralis* female was later used in the first cross represented in the first table in addenda.

EXPLANATION OF PLATES.

PLATE XIX.

- FIG. A. *Adalia melanopleura* Leconte.
 FIG. B. *Adalia annectans* Crotch.
 FIG. C. *Adalia annectans* Crotch.
 FIG. D. *Adalia humeralis* Say.
 FIG. E. *Adalia coloradensis* Casey.
 FIG. F. *Adalia annectans* Crotch.
 FIG. G. *Adalia melanopleura* (more albinic form).
 FIG. H. Pupa of *A. annectans*, *melanopleura*, *coloradensis*, and *humeralis*.
 FIG. I. Larva of *A. annectans*, *melanopleura*, *coloradensis* and *humeralis*.
 FIG. J. Eggs of *A. annectans*, *melanopleura*, *coloradensis* and *humeralis*.
 All drawings are magnified 5 diameters.

PLATE XX.

FIG. 1 shows in diagram the results of the foregoing experiments in inheritance between *annectans*, *melanopleura*, *coloradensis*, and *humeralis*. The numerals beneath the circles in each case indicate the number of individuals in that class. The lines connecting with higher circles indicate parentage in each case.

FIG. 2. *a* and *b*—characters of *annectans-humeralis* female, mated with males indicated.

c to *j*—elytral characters of *annectans* offspring.

k to *n*—pronotal characters of *melanopleura* and *annectans* offspring.
 Numerals indicate number of individuals in the class in each case.

FIG. 3. *a*—elytral characters of *annectans* mother, mated with male indicated.

b to *o*—elytral characters of *annectans* offspring.

p to *v*—pronotal characters of *annectans* offspring.

Numerals indicate number of individuals in each class.

PLATE XXI.

FIG. 4. *a* and *b*—characters of *melanopleura annectans* mother mated with male indicated.

c to *l*—elytral characters of *annectans* offspring.

m to *t*—pronotal characters of *annectans* offspring.

u to *v*—pronotal characters of *melanopleura* offspring.

Numerals indicate number of individuals in each class.

FIG. 5. *a* and *b*—characters of *melanopleura-annectans* mother, mated with male indicated.

c to *d*—pronotal characters of *annectans* offspring.

e to *k*—elytral characters of *annectans* offspring.

l to *r*—pronotal characters of *melanopleura* offspring.

Numerals indicate number of individuals in each class.

FIG. 6. Shows the curves representing the variation in the elytral characters of the *annectans* offspring, drawn in the foregoing figures. The numerals on the left show the number of individuals. The degrees of melanism are designated by the legend below in each case, the most albinic being at the extreme left and the most melanic at the right. "Confluence 1/2" means one case of tendency to confluence, "confluence 2/3" means two cases of tendency to confluence. The latter is here given a rank of its own as it does not seem equal in melanism to one full confluence. The curve above the legend "spot 6 absent" does not represent all the individuals lacking that spot, but only those with no case of confluence.

Curve (a) represents the series in Fig. 2, Plate II. The full line shows the position of the mother in this series.

Curve (b) represents the series in Fig. 3, Plate II. The broken line triangle represents the position of the mother.

Curve (c) represents the series shown in Fig. 4, Plate III.

Curve (d) represents the series shown in Fig. 5, Plate III.

The mother of the series for curves (c) and (d) were *melanopleura* and so have no place in this diagram.

PLATE XXII.

FIG. 7 shows the curves for the pronotal series.

Curve (a) represents pronotal characters of *annectans* offspring shown in Fig. 2, Plate II.

Curve (b) represents pronotal characters of *melanopleura* offspring in Fig. 2, Plate II.

The open triangle represents the mother of the series represented by curves (a) and (b), Fig. 2, *a* and *b*, Plate II.

Curve (c) represents the *annectans* series in Fig. 3, Plate II.

Curve (d) represents the *annectans* series in Fig. 4, Plate III.

Curve (e) represents the *annectans* series in Fig. 4, Plate III, according to general melanism.

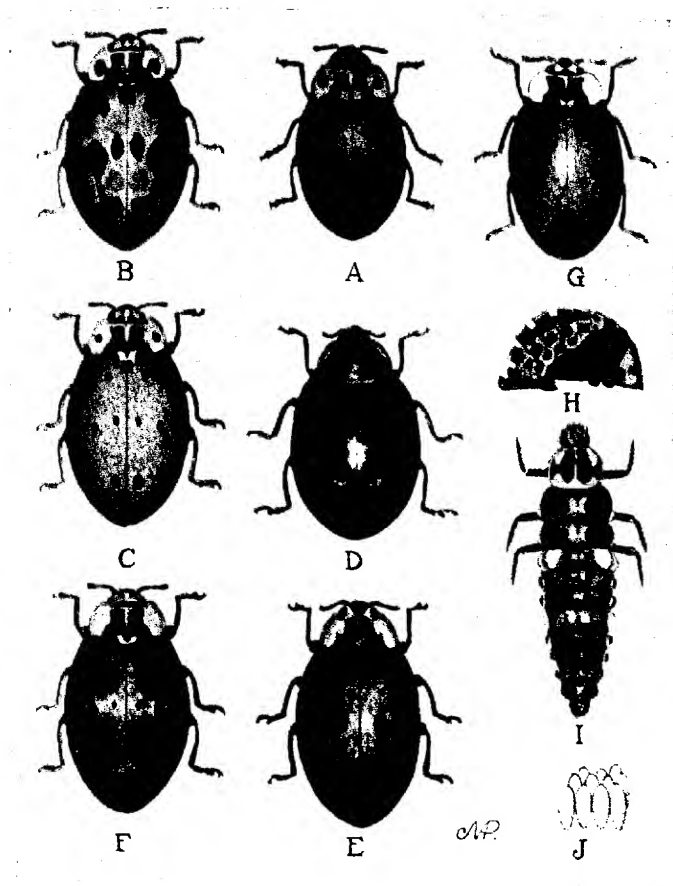
Curve (f) represents the *melanopleura* series in Fig. 4, Plate III.

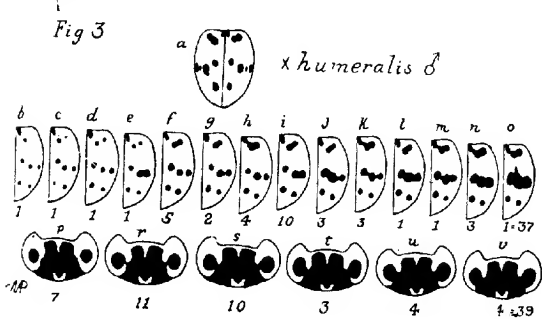
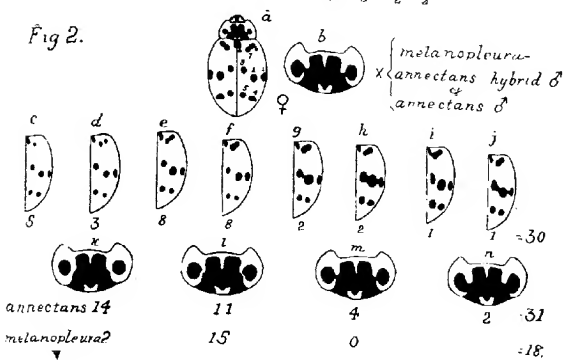
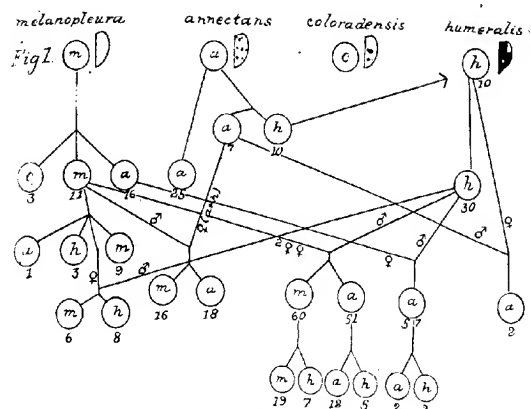
The open triangle represents the mother, Fig. 4, *a* and *b*, Plate III.

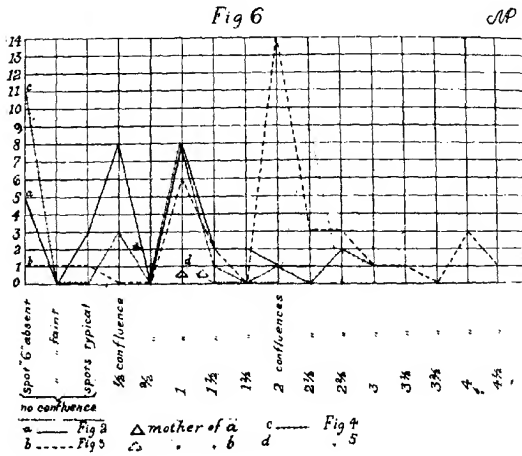
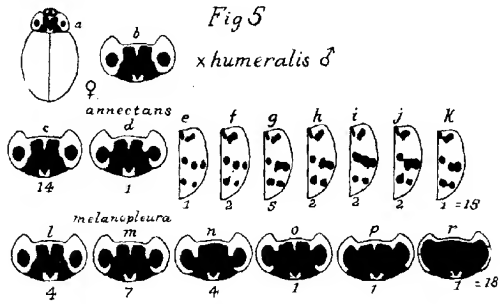
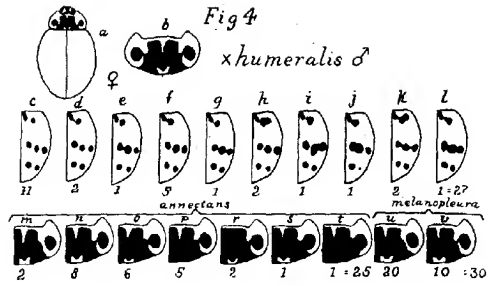
Curve (g) represents the *annectans* series, Fig. 5, Plate III.

Curve (h) represents the *melanopleura* series, Fig. 5, Plate III.

The solid triangle represents the mother Fig. 5 (a) and (b), Plate III.







SPECIFIC CHARACTERS USED IN THE GENUS PSEUDOCOCCUS.

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INTRODUCTION.

The purpose of this investigation was to determine the value of the specific characters used in the descriptions of species of *Pseudococcus*. While all characters used have probably not been noted and while some of those omitted may be of considerable value still the more common and important characters have received attention.

The investigation has been limited to five species,* namely: *agrifoliae* Essig, *citri* Risso, *crawii* Coq., *longispinus* Targ., and *obscurus* Essig. A large number of individuals in each species has been used giving a comparative study for specific variation.

The writer wishes to thank Professor Alex. D. MacGillivray for the many invaluable suggestions given.

TABULATION AND STUDY OF CHARACTERS.

An examination of the descriptions of species in this genus shows a great similarity in the characters used. Provided that these characters do not vary beyond certain limits, this would make the identification of the species easier. However, if these characters vary to any great extent and overlap and merge into each other, the adherence by systematists to these characters instead of the introduction of new ones is unfortunate, and would make the identification of species very difficult, if not impossible. In that case the most valuable data in the descriptions would be the locality and host-plant data.

BODY. 1. Size.—In the great majority of descriptions, the length and width of the body is given. In the measurements given, a great variation in the length of each species is noted.† Lengths such as 3–4 mm., 2–5 mm., 1.5–4 mm., are very frequent, showing the wide variation noted by those describing species. The tables‡ showing the lengths of the body, (Tables 1, 2, 3, 4, 5) in the five species studied do not show a variation any greater than this. A variation of from one and one-half

* The writer does not express an opinion upon the validity of these species.

† R. Mathewson. Can. Entom. XXXIX, p. 286.

‡ In these and the following tables an ocular micrometer with a 2.5 and 1.8 inch objective were used. All measurements are given in microns.

to twice the length of the smaller specimens is shown. A greater variation would probably be found if a larger number of specimens were measured.

TABLE 1. *PSEUDOCOCCUS OBSCURUS* ESSIG.

Specimen	Length of Body	Length of Setal-loop	Length of Setae of Anal-lobes		Length of Setae of Anal-ring
I	2736	544	152	136	176
II			152	152	168
III	2784		160	160	184
IV	2526	736	152	144	192
VI	2304	720	152	148	190
IX	3120	560	156	146	185
XI	2040	320	136	135	176
XII	2688	848	137	145	168
XIII	3000	696		152	167
IVX	3072		150	142	168

TABLE 2. *PSEUDOCOCCUS AGRIFOLIAE* ESSIG.

Specimen	Length of Body	Length of Setal-loop	Length of Setae of Anal-lobes		Length of Setae of Anal-ring
I	2028	1160	221	216	240
II	3312	1129	224	223	200
III	4200	1165		208	184
V	3336		182	184	176
VII	4205	120	208	225	292
X	2928	400	200		200
XIII	3120	405		215	248
XVII	4080		208	203	208

TABLE 3. *PSEUDOCOCCUS CITRI* RISSO.

Specimen	Length of Body	Length of Setal-loop	Length of Setae of Anal-lobes		Length of Setae of Anal-ring
I	3120	416	162	178	108
II	2304	256	180	163	108
III	2526		245	223	120
IV	2808		216	209	129
V	2664	448		228	118
VI	2448	240	221	216	117
VII	3144		181	182	120
VIII	2328		192		115
IX	2662	144	235	216	125
X	2712		225	233	130

TABLE 4. *PSEUDOCOCCUS CRAWII* COQ.

Specimen	Length of Body	Length of Setal-loop	Length of Setae of Anal-lobes		Length of Setae of Anal-ring
	3048	98	228	245	144
IV	2184	101	241	239	168
V	2160	120		200	154
A	2256		216	215	176
B	2160			256	192
VI	2165			248	201
VII	2208	108	208	201	169
VIII	2376		200	176	160
IX	2373		224	222	184
X	2448		223	220	160

TABLE 5. *PSEUDOCOCCUS LONGISPINUS* TARG.

Specimen	Length of Body	Length of Setal-loop	Length of Setae of Anal-lobes		Length of Setae of Anal-ring
I	2088		132	120	139
II	2160		130	124	132
III	1944		96	108	120
IV	2328		95	113	121
VI	2664		113	121	132
VII	2692		127	128	137
VIII	2952		125	123	144
X	3312		228	126	131
A	2950		120	119	133
B	2526		115	122	131

Also only the larger individuals were studied because of the danger of including those in the nymphal stage. Each species was collected from the same or neighboring host plants and were apparently under similar conditions, so that size cannot be taken as a specific character of any great importance. These measurements were taken from mounts. If unmounted specimens were used, the variation would probably be still greater, as then a second factor, namely, the amount of secretion present, would enter. Because of the great variation in size of the different individuals in a species the size of a specimen can be of but little if any value in specific determination.

2. Shape.—In descriptions the shape of the body is variously given as *elongate-ovate*, *rounded-oval*, *convex*, *tapering at ends*, *elongate*, etc., words which are nearly synonymous. A few species are stated to be considerably out of the ordinary

in shape, but in general synonyms are used in the descriptions of body shape. In the species studied, this could not be an important specific character as all the species studied were of practically the same shape. However, in some species, this might be a distinguishing character.

3. Color.—In descriptions the color of specimens is usually given, being stated as, whitish, greyish, pinkish, with a red tinge, etc. The dermis of specimens in this genus is red. The color of the insect depends on the extent that this dermis is hidden by the waxy secretion. The amount of waxy secretion depends largely on the position in which the individual develops. Those in exposed position requiring more of the waxy covering as a protection than those developing in well protected situations. This variation in color is well shown in *agrifoliae* Essig. The color in this species is usually of a reddish, pinkish, or pinkish brown. The writer has found specimens, however, ovipositing in exposed positions which were completely covered with the waxy secretion and through which the red dermis was not visible. Thus all variations from a white to a red specimen were found. In the other species studied the color was normally white. In the five species studied color as a character for separating the species could not be relied upon.

4. Segmentation.—In many descriptions the segmentation is referred to as distinct or not distinct. This is a character that is not used to any great extent. This is fortunate as the value of the prominence of the segmentation as a specific character is extremely doubtful. In mounted specimens it would depend to a large extent upon the method used in preparation. The segmentation in chloroform mounts is well preserved. In caustic potash mounts it would be largely obliterated. In unmounted as well as mounted specimens the age and size of the specimens is of great importance. In nymphs of *Pseudococcus* the segmentation is very distinct. As it passes through its last moult and becomes an adult, this distinctness of the segmentation is lost to a degree. Then as the insect becomes more and more distended with eggs this tendency to lose its prominent segmentation is increased. Also the distinctness of the segmentation in unmounted specimens would depend somewhat upon the amount of secretion covering the insect. With these factors it does not seem that the distinctness of the segmentation can be a very satisfactory specific character.

ANTENNAE.—The number of segments of the antennae is a generic and not a specific character, and so is of no importance in separating species. Several species have been described with seven segmented antennae. The number of segments, eight, of the type of the genus, *longispinus* Targ, has been adopted in this paper. However, a dimorphism has been described in two instances, viz.: by Folsom for *trifolii* Forbes, and by Essig for *agrifoliae* Essig. In these descriptions there is said to be a winter form which has seven segmented antennae; this form giving rise to the summer form with the normal eight segmented antennae. If further investigation shows these observations to be correct, it will be of both specific and generic importance.

The comparative length of the different segments of the antennae is a character that is the most used of any of the characters of the insect's body. The relative length of the segments and the formulae deduced from the measurements is almost invariably contained in descriptions. Sometimes a considerable variation is noted, several formulae being given.

In this study ten specimens of each species were used. Aside from the question of variation which will be taken up later, the relative length of the antennal segments is not a desirable character to use. The greatest difficulty in its use is the difficulty of making correct measurements and the determination of the exact limits of the various segments. The chitin is not continuous from one segment to the next and consequently the portion between the chitinous parts of the segments, the conjunctiva, is not visible or only slightly so in well cleared specimens. Consequently, in making measurements, the determination of the end of a segment will be only approximately at the center of the conjunctiva. This difficulty will be much increased if there are some bends in the antennae. A second difficulty is to determine some point at the end of the segment from which the measurement will always be taken. This difficulty is most apparent with the first segment. This segment is an irregular truncated cone with the sides of different lengths, and but little longer than the width across the base. It will be seen that the determination of the same points for the measurement of this segment would be nearly impossible. In the tables given the writer does not feel that the measurements of the first segment are dependable. Another difficulty in getting dependable formulae is the very slight difference in

the length of some of the segments compared to each other. A difference of only two or three microns is all that is found in some of the segments. It would be exceedingly difficult to eliminate inaccuracies to the extent that the formulae would not be changed by them. Or in other words, the limit of error is so small that error, even with the greatest care, is bound to occur. Unconsciously the measurements would be made to conform to a given formula or to other measurements. The writer continually met this difficulty. The measurements given in Tables 6-10 were taken with an ocular micrometer at a magnification of 660 diameters. Much more accurate work was possible than would have been with a camera lucida.

TABLE 6. *PSEUDOCOCCUS CRAWII* COQ.

Specimen	1st	2nd	3rd	4th	5th	6th	7th	8th	Formulae
I	60	67	74	55	38	46	48	103	83214765
	65	67	77	53	48	41	48	106	83214(75)6
II	67	72	87	48	50	48	48	110	83215(647)
	62	79	84	46	48	46	53	115	832175(64)
III	60	72	74	53	58	46	50	108	83215476
	62	67	79	53	48	48	50	108	832147(65)
IV	70	72	94	55	58	53	48	108	83215467
	70	77	96	46	53	48	48	118	83215(67)4
V	60	72	96	50	60	53	48	115	83215647
	67	74	94	43	58	48	50	117	83215764
VI	62	77	91	46	55	50	50	118	83215(67)4
	65	79	86	48	70	46	48	110	83251(47)6
VIII	62	70	82	53	53	53	46	115	8321(456)7
	62	67	82	50	53	50	50	115	83215(467)
IX	60	67	74	48	55	48	53	108	832157(64)
	60	70	74	48	65	48	53	113	832157(64)
X	60	67	79	48	50	46	50	108	8321(57)46
	58	67	77	48	52	43	48	108	83215(47)6
XI	65	67	72	48	48	53	50	106	832167(45)
	60	69	77	43	48	41	48	106	8321(57)46

An examination of the tables mentioned will show the great variation met with. Following herewith is a discussion of the tables of each species:—

CRAWII COQ. Formula (2, 3, 8) 5, 4, 7, 6, 1, Coq. West Am. Scientist '89.

There is no question about the determination of this species. They were all taken from one plant of white sage (*Ramona polytachia*) at Santa Paula, California. In the tables a formula was found which agrees with the one given by Coquillett. In but one specimen was the formula the same for the right and left antennae of the same individual. All the other formulae differed as much as the specifically diagnostic formulae published for all the species of *Pseudococcus*.

LONGISPINUS TARG. Formula, (2, 3, 8) (1, 4, 5, 6) 7. Newstead, "British Coccidae." Vol. II. The specimens examined were taken from palms in the Horticultural Forcing-house of Cornell University. Of the ten specimens measured, the formulae of the right and left antennae of but one specimen were identical. No formula was found which agreed with the one given by Newstead. The formulae varied as much as the specifically diagnostic formulae published for all the species of *Pseudococcus*.

TABLE 7. *PSEUDOCOCCUS LONGISPINUS* TARG.

Specimen	1st	2nd	3rd	4th	5th	6th	7th	8th	Formulae
I	79 84	79 79	84 84	41 43	53 50	43 43	50 48	101 96	83(12)5746 8(31)257(64)
II	65 67	72 67	79 74	36 38	41 46	88 36	46 43	103 101	83217564 83(12)5746
III	58 60	65 62	63 60	36 36	41 43	38 34	43 41	96 91	82317564 82(13)5746
IV	62 58	62 58	70 70	31 34	48 48	41 38	48 43	108 96	83(21)(75)64 83(21)5764
V	55 58	72 72	67 65	29 36	50 48	29 43	43 46	106 106	823157(46) 82315764
VI	62 60	72 77	74 74	43 46	60 58	46 48	48 48	106 106	83215764 82315(76)4
VII	74 72	72 82	74 91	48 50	62 62	43 46	43 48	101 103	8(13)254(67) 83215476
VIII	65 70	67 72	70 70	43 41	50 46	41 43	43 46	98 96	83215(47)6 82(31)(75)64
IX	55 60	65 65	65 65	36 34	48 50	38 41	46 43	101 101	8(32)15764 8(23)15764
X	62 62	72 70	65 65	43 41	58 48	41 43	48 43	101 103	82315746 82315(76)4

TABLE 8. PSEUDOCOCCUS AGRIFOLIAE ESSIG.

Specimen	1st	2nd	3rd	4th	5th	6th	7th	8th	Formulae
I	94	77	74	50	55	50	48	108	81235(1)7
	89	82	74	53	55	53	48	115	81235(1)7
II	72	72	74	48	58	48	41	106	83(21)5(46)7
		74	72	48	48	53	53	108	
V	72	79	72	48	48	48	50	113	82(13)5(45)6
	72	79	72	48	53	53	43	110	82(13)5(46)7
VII	72	82	72	53	60	50	48	115	82(13)5(46)7
	72	82	70	53	60	50	53	118	82135(47)6
VIII	74	72	74	89	48	53	108		74(13)265
	72	70	79	89	48	98	98		(76)43125
XIII	74	91	82	65	70	55	48	113	82315(46)7
	77	84	82	65	72	60	53	115	82315(46)7
XIV	82	82	74	53	60	53	55	110	8(12)357(46)
	79	79	77	50	65	50	50	120	8(12)35(46)7
XVI	77	84	74	55	60	50	53	115	82135(46)7
	74	79	74	50	62	58	50	110	82(13)5(46)7
XVII	72	77	72	53	60	53	50	115	82(13)5(46)7
	72	82	74	55	55	53	46	110	8231(45)67

AGRIFOLIAE ESSIG. No formula is given in the description. The description refers however to the figures of the antennae for the relative length of the segments. Measuring the figure, the following formula is constructed, 7, 1, 3, 2, 4, 6, 5. The figure is evidently taken from a nymph, as this species has normally eight segmented antennae. These specimens were all taken from a single oak tree (*Quercus agrifoliae*) at Santa Paula, California, and are from the lot of specimens that the type of the species was taken. In two specimens the formulae of the right and left antennae were found to be the same although the formula of each specimen is different. The formulae of the twenty antennae varied as much as the specifically diagnostic formulae published for the species of *Pseudococcus*.

TABLE 9. *PSEUDOCOCCUS CITRI* RISSO.

Specimen	1st	2nd	3rd	4th	5th	6th	7th	8th	Formulae
I	67 62	60 60	58 60	41 43	41 43	41 48	43 48	101 103	81237(456) 81(23)(67)(45)
II	55 60	60 58	55 50	38 36	36 41	46 38	46 43	103 101	82(13)(67)45 81237564
III	60 60	67 65	72 72	41 41	48 48	46 46	55 53	106 108	83217564 83217564
IV	60 65	65 60	60 62	36 36	41 36	36 38	50 48	110 108	82(13)75(64) 813276(54)
V	60 58	62 62	67 65	36 36	48 43	43 43	53 50	113 113	83217564 83217(65)4
VI	65 62	72 72	67 65	46 48	48 46	48 50	50 53	103 110	82317(56)4 82317645
VII	67 67	60 58	67 60	36 38	38 41	41 43	48 43	106 98	8(13)27654 8132(67)54
VIII	67 72	72 62	67 67	38 41	43 48	43 43	46 48	108 103	82(13)7(65)4 8132(75)64
IX	60 60	67 65	60 60	43 43	43 41	38 46	41 43	96 96	82(13)(45)76 82(13)6(74)5
X	67 67	67 65	72 67	41 43	41 48	41 46	50 48	108 108	83(12)7(456) 8(31)2(75)64

CITRI RISSO. Formula 6, 3, 2, 1, 5, (4, 6, 7) Newstead, "British Coccidae" Vol. II. The specimens of this species were taken from coleus in the Horticultural Forcing-houses of Cornell University. No formula was found that agreed with the one given by Newstead. In one specimen the formulae for the right and left antennae were identical. The formulae of the twenty antennae varied as much as the specifically diagnostic formulae published for all the species of *Pseudococcus*.

OBSCURUS ESSIG. Formula 8, 1, 3, 2, 4, 7, 5, 6. Essig, "Pomona Jour. Ent." '09. The specimens of this species were taken from an elder tree (*Sambucus glauca*) at Santa Paula, California, and are from the lot of specimens that the type for the species was taken. In one specimen the formulae of the right and left antennae were identical.

TABLE 10. PSEUDOCOCCUS OBSCURUS ESSIG.

Specimen	1st	2nd	3rd	4th	5th	6th	7th	8th	Formulae
I	84 65	72 67	77 65	41 53	58 58	41 96	53	103	813257 (4) 62(31)57
II	84 72	72 75	79 84	48 43	55 53	46 43	48 48	84 98	(81)3257 (7)6 832157 (64)
III	82 72	79 79	84 79	29 38	60 53	50 46	53 50	101 103	831257 (4) 8(32)15764
IV	82 77	89 79	84 86	48 48	65 65	50 48	50 48	108 108	823157 (7)4 832157 (64)
V	80 74	86 84	91 96	53 50	58 65	48 55	50 48	113 113	83125476 83215647
VI	79 74	74 72	82 82	38 36	65 60	41 41	50 48	106 98	83125764 83125764
VII	77 89	82 74	84 71	38 41	53 53	41 41	50 46	108 106	83215764 81(23)57 (64)
VIII	84 84	89 84	89 96	53 48	67 70	48 41	53 50	108 110	8(32)15746 83(21)5746
IX	72 65	79 65	74 60	41 46	60 53	48 146	53	106	82315764 6(12)354
X	84 86	72 74	84 84	48 46	58 60	46 34	55 60	55;43 108	(13)25(78)469 8132(75)46

No formula was found agreeing with the one quoted. In specimen X the right antenna has nine segments and in specimen IX the left antenna has six segments. An examination of Table I shows that this specimen is the largest specimen studied, and as it was found in an egg mass it was undoubtedly an adult. Specimen I, which will be seen to be of normal size (Table I), also had the left antenna with six segments. This variation in the number of segments was also noted in other specimens. The formulae of the twenty antennae measured varied as much as the specifically diagnostic formulae for all the species of *Pseudococcus*, as well as one formula placing the specimen in the genus *Phenacoccus* and two formulae placing the specimens in the genus *Ripersia*.

From the above review it will be readily seen that the relative length of the segments of the antennae are valueless as specific characters. Other workers as well have found this

character very variable. Kellogg & Smith, '04, found that in twenty-five specimens of *Cerepato yuccae*, a closely allied genus, no two formulae agreed, "and that there was practically as much variety in these formulae as there is among the eleven formulae published as specifically diagnostic for eleven North American species of the genera *Cerepato* and *Phenacoccus*." Again Tinsley, J. D., '08, in discussing the variation in the antennae of *P. virgatus* Ckll. gives eleven different formulae. Again the same author, 1900, in his description of a new species, *P. texensis* Tins., gives three different formulae. Ehrhorn, Edw. M., 1900, in his description of a new species, *P. maritimus* Ehr., gives four formulae. The universal use of antennal formulae in descriptions is unfortunate, as this has given an excuse for the creation of new species and is valueless in analytical tables for the determination of specimens. The sooner that the valuelessness of this character is realized by systematists describing new species of this genus, the sooner will a search for valuable characters be begun and a serious mistake in taxonomy be corrected.

LEGS. Tables 11-15. The length of the legs is used to quite an extent in descriptions. Their length compared to the length of the antennae is often stated, also the length of the different segments compared with each other. They are often spoken of as long and strong. The presence of hairs is often noted, also that of knobbed digitules.

For the study of the legs five specimens of each species were used. They were the same specimens that were used in the study of the antennae. The measurements of the different segments are the greatest length of these segments, so that the sum of the lengths of the different segments will be greater than the length of the leg. Like the basal segment of the antennae, the coxa is very difficult to measure and the results are not entirely reliable.

At the right hand side of the tables, formulae are appended. These formulae are constructed in the same manner as the antennal formulae. The segments are numbered in order beginning with the coxa.

The formulae show but little if any more satisfactory results for specific determination than do the formulae of the antennae. The formulae of each pair of legs for each of the species will be discussed together.

Prothoracic Legs. In *crawii* Coq. and *citri* Risso the third segment is always the longest, the fourth segment coming next in order. In the remaining three species the third segment is usually the longest but may be equal to or less than the fourth segment. The first segment is always third in order in the formulae. In no species does the second segment bear any fixed relation to the fifth. The sixth segment is always much the shortest and comes last in order in the formulae.

Mesothoracic Legs. In *crawii* Coq. the third segment is always the longest. In the other species the position of the third and fourth segments vary in relation to each other. The first segment always comes third in the formulae. The second and fifth segments vary in relation to each other in each of the species. The sixth segment always comes last in the formulae.

Metathoracic Legs. In *obscurus* Essig and *citri* Risso the fourth segment is usually longer than the third. In *obscurus* Essig an exception is seen to this in the right leg of Specimen XI. In *obscurus* Risso an exception is seen to this in specimen VII. In the other species the fourth segment is always longer than the third. The first segment always comes third in the formulae. In no species do the second and third segments bear any fixed relation to each other. The sixth segment is always much the shortest and comes last in the formulae.

It will be seen from the above discussion that the variation in the formulae is too great for them to be of service in specific determination. Exceptions are found to any generalization that might be made. The limits within which there can be variation are so small that the variations are almost sure to go beyond these limits. Other parts of the legs as setae, digitules, etc., apparently offer no characters of a specific nature.

TABLE 11. PSEUDOCOCCUS CRAWII COQ.

Segment	Specimen	Side	Coxa	Tr.	Femur	Tibia	Tarsus	Claws	Formula
Prothoracic	I	Rt.	192	120	288	252	114	39	341256
		Lft.	198	120	288	252	108	36	341256
	IV	Rt.	240	126	312	248	120	42	341256
		Lft.	228	120	318	276	120	42	341(25)6
	V	Rt.	228	120	276	240	108	42	341256
		Lft.	222	120	270	240	108	42	341256
	VIII	Rt.	210	120	276	216	108	30	341256
		Lft.	210	120	282	216	108	30	341256
	IX	Rt.							
		Lft.	204	114	288	252	114	36	341(25)6
Mesothoracic	I	Rt.	204	120	312	264	114	39	341256
		Lft.	210	126	312	270	114	42	341256
	IV	Rt.	246	120	324	306	120	42	341(25)6
		Lft.	234	126	336	312	120	42	341256
	V	Rt.	240	120	300	276	114	42	341256
		Lft.	228	120	300	282	114	42	341256
	VIII	Rt.	216	120	294	270	114	33	341256
		Lft.	222	120	300	270	114	33	341256
	IX	Rt.	210	120	294	276	120	36	341(25)6
		Lft.	216	120	300	288	120	36	341(25)6
Metathoracic	I	Rt.	222	126	330	342	114	42	431256
		Lft.	222	126	330	336	114	45	431256
	IV	Rt.	252	132	360	390	132	48	431(25)6
		Lft.	258	138	348	390	132	48	431256
	V	Rt.	240	126	330	360	120	42	431256
		Lft.	240	126	330	360	120	42	431256
	VIII	Rt.	216	126	306	336	126	36	431(25)6
		Lft.	216	126	306	354	126	36	431(25)6
	IX	Rt.	240	132	336	366	132	39	431(25)6
		Lft.	240	132	342	360	132	39	431(25)6